ECOLOGY

Vol. 40 APRIL, 1959 No. 2

SOME FEATURES OF THE ECOLOGY OF BUFO PUNCTATUS IN DEATH VALLEY, CALIFORNIA[1]

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Until now knowledge of the red-spotted toad (*Bufo punctatus*) has been limited to its distribution and general facts pertaining to its life history and ecology. The observations of Camp (1916), Engelhardt (1917), Little and Keller (1937), Miller (1944), and Johnson *et al.* (1948) have been summarized by Wright and Wright (1949) and by Stebbins (1951). A review of these papers would only emphasize the limited nature of our knowledge of the ecology of this amphibian. Such a situation is entirely understandable for neither the distribution nor the behavior of the red-spotted toad is conducive to a detailed ecological study.

The following discussion will deal with certain features of the ecology of red-spotted toads which have hitherto been lightly treated or ignored and will add some details to ideas which have already been advanced.

Bufo punctatus was first discovered in California at Furnace Creek Ranch in Death Valley by members of the Death Valley Expedition of 1891 (Stejneger 1893). Since that time Storer (1925), Miller (1944), and Johnson *et al.* (1948) have reported populations elsewhere in southeastern California, but this paper deals with a population of toads in Death Valley, only a few miles from Furnace Creek Ranch.

THE STUDY AREA

The study upon which this report is based was carried out while the writer was employed by the United States National Park Service during 1954 and 1955. The population investigated inhabits the Cow Creek residential area, a group of government residences located on an alluvial fan at an elevation of approximately 160 feet above sea level, about one mile from the winter headquarters of the National Park Service and 5 miles north of Furnace Creek Ranch. The residential area is located at 2 levels: the upper level or "mesa," and the lower level just north of and below the mesa.

The water supply for this community is piped from Nevares Spring which arises 2 miles east of the village at the base of the Amargosa Range. Water is introduced into irrigation ditches on the mesa from a hydrant and this water flows north from the mesa and into a shallow drainage ditch flowing west from the lower part of the village. Water is also piped to a water-powered light plant, housed on the lower level of the area, and flows from this building into the drainage ditch mentioned above. About 100 yards west of the lower portion of the village a gardener's shack stands at the east end of what was at one time a nursery. The old irrigation ditches of the nursery still conduct water from the main drainage ditch through this area when the flow of water from the village is heavy. The main drainage ditch parallels the road for about three-tenths of a mile west of the village at which point water is diverted to the north and over a small waterfall into the original channel of Cow Creek. Water reaching this point flows for only a short distance at the surface before it disappears into the ground (Figure 1). The flow of water in the irrigation ditches is irregular and, because the water-powered generator is also run on an irregular schedule, the ditches may be dry for several days at a time.

The natural vegetation of the Cow Creek residential area includes honey mesquite (*Prosopis juliflora*) and arrow weed (*Pluchea sericea*). Lawns are now maintained in some parts of the lower part of the village and tamarisks (*Tamarix gallica*) have been planted in all parts of the area. Along the drainage ditches yerba mansa (*Anemopsis californica*) grows and to the west of the village arrow weed and reeds (*Phragmites communis*) are dense near the water.

[1] Contribution No. 10 from the Department of Biology, Wayne State University, Detroit 2, Michigan.

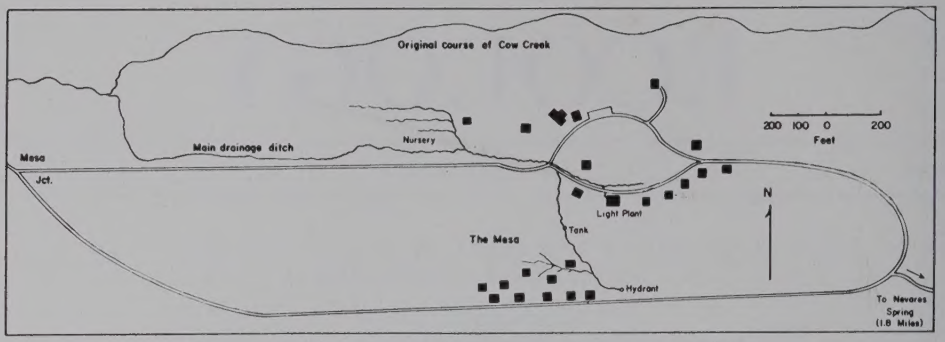

FIG. 1. The Cow Creek residential area, Death Valley National Monument, California.

EMERGENCE AND BREEDING ACTIVITIES

There is a period during the winter when the toads, presumably dormant, are neither seen nor heard but in the spring (usually in March) they become active again. I cannot state with certainty the time of emergence because it is possible that the toads emerge a short time before calling commences. Furthermore, there may be a period of early activity (*e.g.* in February) followed by inactivity before breeding activities are initiated. For example, in 1954 toads first called in the Cow Creek area at 7 p.m. on February 23. There followed about a week of activity and then approximately three weeks of inactivity and it was not until March 26, that breeding was really initiated. In 1955 calling was first noted in the Cow Creek area at 7:55 p.m. on March 8. There is a possible correlation between these events and mean daily temperature (Figure 2). Mean daily temperatures below 70° F (21.1° C) do not seem to be conducive to breeding activity.

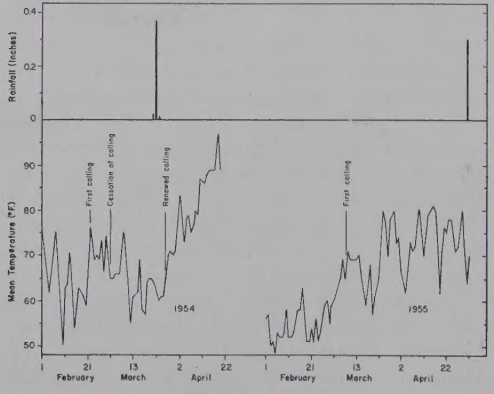

FIG. 2. Vocality of *Bufo punctatus* and mean daily temperatures and total rainfall (February 1-April 20, 1954; and February 1-May 2, 1955) at Cow Creek, Death Valley, California.

Red-spotted toads are active at night and remain concealed during the day. On March 17, 1954, at 5 p.m., I found 7 toads beneath planks in the vicinity of Nevares Spring. In the residential area children occasionally found toads during the day under boards or more commonly in the covered subterranean recesses around water control faucets. The toads emerge about dusk (the earliest times at which I heard trilling were 6:20 p.m. on March 27, 1954; 6:44 p.m. on April 2, 1954; and 6:46 p.m. on April 7, 1954) and may remain active and continue to trill until as late as 2 a.m. Observations were not made at later hours.

Male toads call vigorously from posts along the edge of ditches or near standing water. The call is a series of high-pitched musical trills of relatively short duration as has been described by Stebbins (1951). On April 1, 1954, I recorded the following pattern:

5-30-5-30-5-115-3-10-5-10-7-120-4-15-3-21-2-25-7-118-6-20-5-27-3 in which the initial figure represents the duration of the trill in seconds and after which the duration of periods of silence and trilling alternate. One may observe that the trills are only from 2 to 7 seconds in duration and may be separated by as long as 2 minutes. Other patterns recorded were similar to the one recorded above except that occasionally trills as long as 10 to12 seconds were heard. The trills of 2 or more males sometimes alternated but on other occasions occurred simultaneously so that there is apparently no organized pattern involving 2 or more calling individuals. Toads that are handled often emit bird-like cheeps.

Amplexed pairs were first observed on April 1 in 1954 and on March 11 in 1955. During the 2 seasons a total of 9 pairs was observed, 7 of which were in water (either in an irrigation ditch or in a pool or puddle) and 2 on the ground. One of the latter pairs was on the move with the male

being carried on the female's back. Males may attempt to amplex other males but are apparently warned off by loud trilling and struggling by the molested male. Amplexus is inguinal.

My observations were suspended on April 20, 1954, and May 1, 1955, and no eggs had been deposited by these dates. Storer (1925) quotes Grinnell as stating that spawning occurred at the end of the first week of April in 1917 at Furnace Creek Ranch.

Of 165 toads observed in the Cow Creek area during 1954 and 1955, 127 were in water. Of the other 38, 19 were located on a damp substrate, 16 on a dry substrate and 3 on grass. The distribution of 47 water and substrate temperatures is summarized in Table I.

TABLE I. Water and substrate temperatures associated with 47 *Bufo punctatus* in Death Valley, California

	Numbers of Toads		
	15-20° C	20.1-25° C	25.1-30° C
Water	8	19	7
Substrate	5	8	0

POPULATION SIZE

It seemed that an investigation of the size of the Cow Creek population might prove particularly fruitful. With this end in mind 34 toads were marked by toe-clipping between February 23 and April 19, 1954. No more than 2 toes were cut from any toad and thumbs were not excised. Censuses of the area inhabited by the population were made on April 1, 3, 4, 6, 7, 14 and 19. The data derived from these censuses are summarized in Table II.

TABLE II. 1954 census data pertaining to a population of *Bufo punctatus* in Death Valley, California

Date	Number of Captures (w)		Proportion of catch previously handled (y)	Total number previously marked (x)
	New	Previously marked		
Feb. 23	3	0	.00	0
April 1	8	1	.11	3
April 3	6	1	.14	11
April 4, 6	13	11	.46	17
April 7	3	7	.70	30
April 14	1	10	.91	33
April 19	0	2	1.00	34

The data are arranged in a manner suggested by Hayne (1949). The formula $P = \frac{\Sigma wx^2}{\Sigma wxy}$ (where P is the population estimate) permits an averaging of the data and yields a population estimate of 37.

In 1955 twenty-three additional toads were marked and censuses were carried out between March 11 and May 1. If it is assumed that all of the 34 toads marked in 1954 survived until the spring of 1955 one arrives at a population estimate of 67 using Hayne's method. This assumption does not seem to lead to a realistic approach to the problem and, in an attempt to assess the population size more accurately, the unmarked fraction of the 1955 population has been analyzed separately. Data from 1955 censuses (in which the recapture of toads marked in 1954 have not been recorded) are presented in Table III.

TABLE III. 1955 census data pertaining to a population of *Bufo punctatus* in Death Valley, California

Date	Number of Captures (w)		Proportion of catch previously handled (y)	Total number previously marked (x)
	New	Previously marked		
March 11	6	0	.00	0
March 13	5*	1	.17	6
March 24, 26	1	1	.50	10
March 27	1	1	.50	11
March 28	5	7	.58	12
April 12	2	5*	.71	16
April 14, 15	3	9	.75	18
May 1	1	4	.80	21

*one dead

These figures yield a population estimate of 24.

Then the total population in 1955 presumably was made up of approximately 24 unmarked toads plus some surviving fraction of the 34 toads marked in 1954. It may be observed that if the unmarked fraction of the population in 1955 was about 24 toads then the 23 toads marked in 1955 represent about 95 per cent of the unmarked toads at large in the population at the beginning of the 1955 season. It seems reasonable to assume that a similar proportion of the toads marked in 1954 was also recovered in the course of the 1955 censuses. Fourteen of the original 34 marked were recaptured in 1955. The above reasoning leads us to conclude that only about 15 of the 34 toads marked in 1954 were still at large in the population in 1955. The loss is probably due entirely to mortality (I cannot visualize emigration as influencing the size of this population significantly). Natural causes of mortality are unknown to me but 2 toads were found which had been run over by cars.

Thus, the population in 1955 would seem to have been made up of about 40 toads; hardly a significant increase over the 1954 level.

I estimate that the actual area occupied by these toads is on the order of 5 acres mostly associated with the half-mile of open ditches within and west of the village. Hence the ecological density of toads in this population is about 8 toads per acre.

Only a few workers have collected sufficient data to justify an estimate of the size of an anuran population. Jameson (1955) has approximated the size of some colonies of *Syrrhophus marnocki* in Texas and Martof (1956) drew guarded conclusions as to the number of green frogs in a Michigan population. In these cases the difficulty of the problem was intensified by the fact that the population was large and dispersed over an extensive area so that immigration and emigration occurred with appreciable frequency. Pearson (1955) was probably more successful in his work with *Scaphiopus h. holbrooki* in Florida because of the restricted ranges of these toads and the relatively small number of individuals involved in his study.

The isolated colonies of *Bufo punctatus,* which seem to be characteristic of the distribution of this toad, afford an admirable opportunity for the analysis of changes of anuran population size and structure. Here the complications associated with a large population, a large area, and extensive movements, are non-existent. One may examine a population over successive years with reasonable confidence that any changes in population size reflect a lack of balance between replacement and mortality. Furthermore the total area occupied by the population is small and suitable habitats within this area further restricted so that a series of censuses actually constitute a sampling of the entire population.

These considerations lead me to conclude that the population of *Bufo punctatus* under consideration was made up of about 37 individuals in 1954 and that approximately 15 (40%) of these toads survived until 1955. However, the survival of toads transforming during the summer of 1954 was such that the population was maintained at its 1954 level. This suggests that about 60% of the population is made up of first-year toads but I have no direct data to support this. The toads were not measured and I was not conscious of distinct size-classes. Actually the first-year toads *may* be separable from older toads on a size basis —Johnson *et al.* (1948) found that 46 male *Bufo punctatus* from Pachalka Springs in the Providence Mountains, California, constituted 2 obvious size classes (40-45 mm and 49-52 mm).

Movements

The points of original capture of toads were recorded on maps of the Cow Creek area. Points of recapture were similarly recorded so that distances moved (assumed to be straight lines) could be calculated. Ninety-two recaptures, involving 40 of the 57 marked toads, were made. One toad was captured 8 times (twice in 1954 and 6 times in 1955) and 39 other toads were recaptured from once to 5 times.

Focal points of activity were found to be a small artificial goldfish pond, the vicinity of the light plant (where there were permanent puddles from leaking pipes), and a small water-filled concrete tank along the course of the ditch running from the top of the mesa to the lower part of the village. When no water flowed in the ditches the toads centered around these features but when the ditches had water in them toads were found quite generally distributed along these watercourses.

The maximum distance moved was about 1200 feet and this movement was effected in 5 days. The magnitude of 78 movements are summarized in Table IV.

Table IV. Magnitude of 78 movements by *Bufo punctatus* in Death Valley, California

	Distance moved (feet)								
	0	10-100	110-200	210-300	310-400	410-500	510-600	610-700	710+
Number of movements.	33	11	9	8	3	5	2	3	4

Movements of 8 toads (captured 5 or more times) are illustrated in Figure 3.

It is not surprising, in view of the size and location of the area occupied by the population, that the movements of these toads are not of great magnitude. Bogert (1947) and Moore (1954), working with other species of the genus *Bufo* have recorded movements of as much as one mile or even as much as 2¼ miles.

It seems that the limited spatial extent of the habitat available to the Cow Creek toads serves to restrict the magnitude of movements. It may be observed (Figure 3) that toads, if they move at all, shuttle back and forth within the area, in an apparently random manner. This sort of behavior may not be entirely due to a restricted habitat. Carpenter (1954) recorded movements of *Rana p. pretiosa* in Jackson Hole, Wyoming, where the available habitat is not drastically limited, and found that:

> when the movements of individuals captured three or more times are plotted the resulting patterns indicate that there is a tendency for individuals to return towards the point of capture.

In view of these facts one would expect the

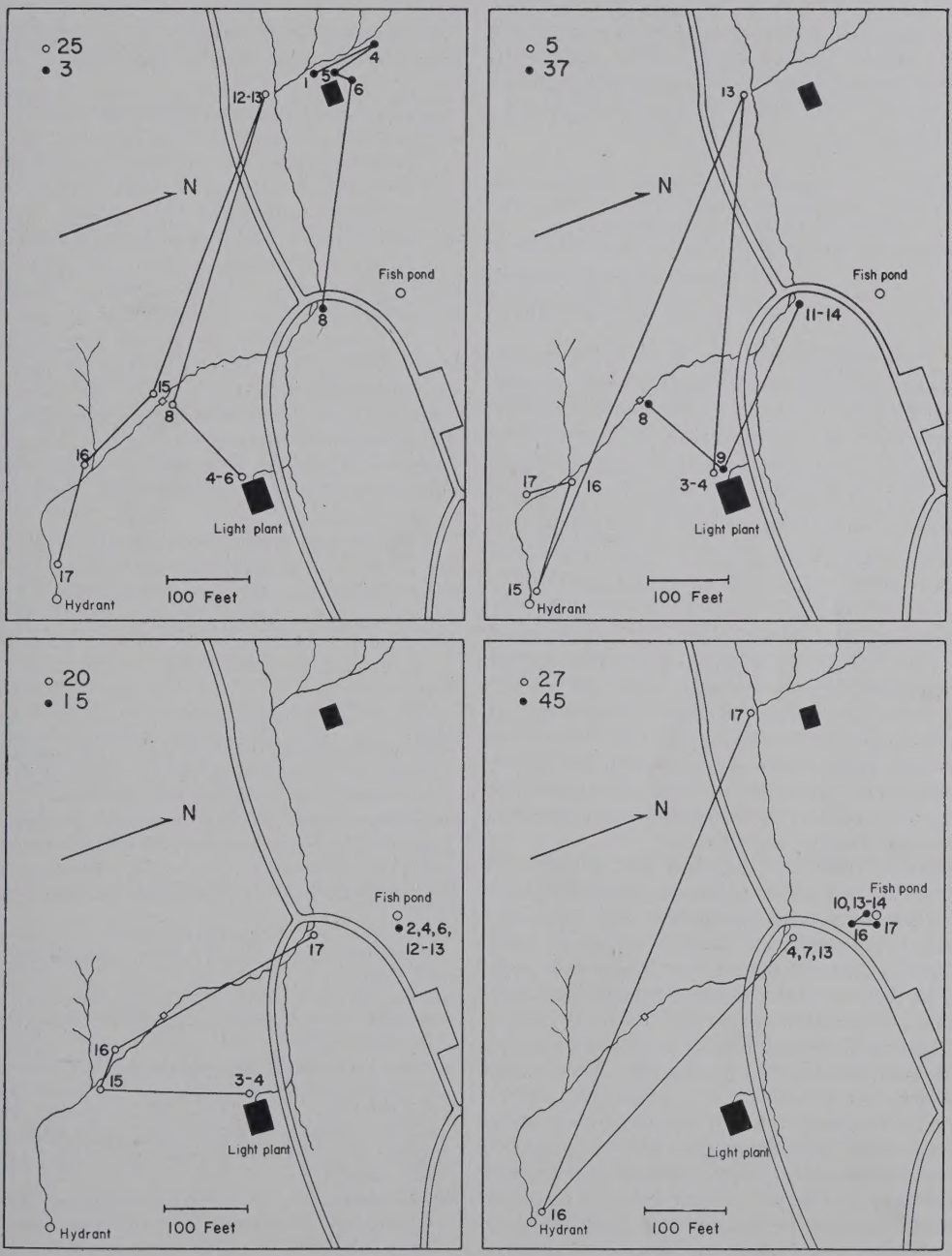

FIG. 3. Movements of 8 *Bufo punctatus* in Death Valley National Monument, California. The small numbers refer to the following 17 dates; in 1954: 1-February 23, 2-April 3, 3-April 4, 4-April 6, 5-April 7, 6-April 14; and in 1955: 7-March 8, 8-March 11, 9-March 13, 10-March 24, 11-March 26, 12-March 27, 13-March 28, 14-April 12, 15-April 14, 16-April 15, 17-May 1.

magnitude of apparent movement to increase as the time elapsed between captures increases only to a point and that beyond this point increased time between captures would not be matched by further increases in the apparent magnitude of movements. That such is the case is suggested by the data in Table V.

TABLE V. Time elapsed between captures and magnitude of apparent movement in 78 movements by *Bufo punctatus* in Death Valley, California

	Days elapsed between movements			
	1-3	4-10	11-20	21-41
Number of movements	28	15	30	5
Range of magnitude of movements (feet)	0-400	0-1200	0-850	60-500
Mean (feet)	60	140	300	280

In such an environment as exists in Death Valley it is hard to envision mechanisms by which genetic exchanges between the various populations of toads may occur. The Cow Creek population is undoubtedly a derivative of the population centered around Nevares Spring and now artificially isolated from the latter by the diversion of water from Nevares Spring through a pipe instead of along the original course of Cow Creek. The only other populations of toads in this part of Death Valley with which I am familiar are at Furnace Creek Ranch and Furnace Creek Inn. These probably represent derivatives of populations presently associated with Texas Spring and Travertine Spring respectively.

Storer (1925) has suggested that the present distribution of *Bufo punctatus* represents populations isolated by the drying of a once extensive system of inland lakes. Death Valley was filled by Lake Manly during the Pleistocene and probably at this time there were populations of toads more or less encircling the lake. The drying of this lake resulted in a number of disjunct populations, each associated with some permanent source of water.

Today floods are the only natural agency which I can envision as permitting genetic exchange between such isolates. Even this mechanism would be likely to operate only in the direction in which water flows along the floor of the valley or down the tributary canyons during floods and populations at the north or south end of Death Valley or near the heads of canyons would not be enriched by flood-borne toads.

SUMMARY

1. Red-spotted toads are active only at night and their activities are usually centered in or near water.

2. Breeding activities seem to be roughly correlated with mean daily temperatures of about 70° F (21.1° C) or above.

3. The Cow Creek population was made up of approximately 37 individuals in the spring of 1954.

4. About 15 individuals survived until the spring of 1955 but the survival of toads which transformed in the summer of 1954 (about 24) was adequate to restore the population to its 1954 level.

5. It is estimated that about 5 acres is available and regularly utilized by these toads. Therefore the ecological density is roughly 8 toads per acre.

6. The magnitude of movements was not found to be great. This reflects, at least in part, the spatially restricted habitat available. The apparent mean distance of movements increases with time elapsed between captures to a point (about 300 feet after 11-20 days) after which an increase in time elapsed between captures does not result in further increase.

7. Death Valley populations of *Bufo punctatus* appear to be genetically isolated colonies derived from a once more extensive Pleistocene distribution associated with Lake Manly.

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TEMPERATURES PREFERRED BY THE PIERID *ASCIA MONUSTE* L.

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INTRODUCTION AND ACKNOWLEDGMENTS

An investigation of the migratory habits of *Ascia monuste* was undertaken during 1949 and 1950. Some of the results have been published (Nielsen and Nielsen 1950, 1952) and a final report, including additional observations in 1954 and 1957, is in preparation.

In the course of these studies it was thought important that the temperature relations of the species be investigated. From August, 1949 to October, 1950 several experiments were made to determine the preferred temperature. Some 16,800 single observations were made, utilizing 181 butterflies.

The apparatus was made in the workshop of the Archbold Biological Station, and we would like to express our most sincere gratitude for the help and interest with which the Director of the Station, Mr. Richard Archbold, supported our work.

We are much indebted to Dr. M. W. Provost for linguistic revision of the manuscript and to Dr. A. M. Hemmingsen for useful comments.

TECHNIQUE

The animal chamber was a trough 120 cm long with bottom 50 mm wide and walls 32 mm high, covered with a glass lid. One end of the chamber was closed by a cooling chamber through which ice water was circulated, the other end by an aluminum block enclosing a heating coil the temperature of which was regulated by a variable transformer. The whole apparatus was within a wooden box insulated with 40 mm of rock wool and so placed that only a few millimeters separated the glass lid of the animal chamber from a similar glass lid on the outer box.

Either a stirring rod or a thermocouple could be introduced into the chamber from the cool end. There were 5 copper-constantan thermocouples in the animal chamber, one in the air above the apparatus, and one in the cooling chamber. The reference junction was kept at room temperature within a thermos bottle. The Weston galvanometer had an internal resistance of 152.3 ohms and a sensitivity of 25 x 10^{-6} amperes. By keeping the external resistance at 10 ohms one division on the galvanometer scale corresponded to one degree centigrade.

On the bottom of the animal trough was an arbitrary scale 47 inches long with a mark at each inch. The thermocouples were at the marks 03, 13, 23, 33, and 43, with the sensitive points protruding 5-10 mm from the walls.

The temperature gradient within the chamber usually extended from 15° at point 03 to 42° at point 43. By introducing a thermocouple and moving it around it was established that the temperature variation within any cross section of the chamber was under 0.5° C.

CALCULATION OF THE PREFERRED TEMPERATURE

The positions of the animals were recorded every time they rested at the same point for more than 2 minutes. If they did not move after about 10 minutes they were stirred with a rod introduced into the chamber through the access at the cooling end. Every preferred temperature datum is thus a temperature at which a butterfly had been observed resting from 2 to about 10 minutes, and, in pooling results, the number of minutes the animals had been observed at corresponding temperatures is given. Each experiment lasted several hours and comprised variable numbers of observations, so, in comparing experiments, we must use the percentage of observations at the different temperatures rather than minutes of resting. In pooling experiments the number of minutes must be used, of course, and the percentages are then derived from total figures.

Temperatures were read every half hour (XX^h15' and XX^h45') and were considered valid for a period of 15 minutes before and 14 minutes

[1] Now: Florida State Board of Health, Entomological Research Center, Vero Beach, Florida.

after the reading. Temperature equivalents of the butterflies positions were derived from graphs prepared for each half-hour observation period.

For the complete expression of preferred temperatures the total number of minutes of observation in the experiment was used. In every experiment there were periods when the butterflies moved around, of course, so that a 3-hour experiment, for example, could total only some 150 minutes of resting observation.

The results of one single experiment are plotted in Figure 1. The S-shaped form of the integrated values suggests a certain similarity to the normal frequency distribution. Herter (1953, p. 69 ff), thus calculates a mean error on his preferred temperature determinations on the assumption that the frequency distribution is normal. However, our unpublished studies on the temperature preferred by *Gryllus domesticus* and the Chalcidian wasp, *Melitobia acaste* Walk., based upon a very large number of observations, did not support the view that the distribution is normal. Neither by substituting arbitrary equi-distant values of the normal distribution integral for the integrated percentages nor by plotting the integrated percentages on probability paper did the function become a straight line; on the contrary, the larger and more uniform the observational material was, the more pronouncedly the S-shape was found to remain. It cannot then be gratuitously assumed that preferred temperature determinations fit a normal distribution pattern.

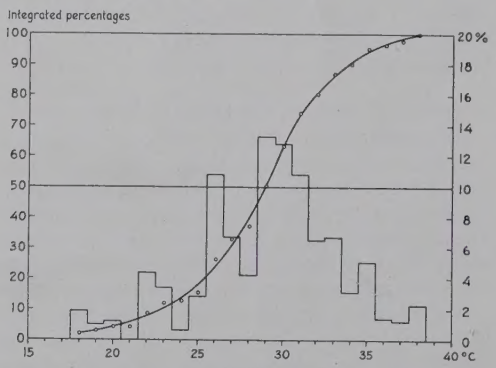

FIG. 1. Frequency distribution of time a butterfly rests at certain temperatures, expressed as % of the total time duration of an experiment. The S-shaped curve referring to the ordinates at left represents the integrated percentages. The abscissa at the point where this curve crosses the 50% ordinate is the preferred temperature by definition,—*in casu* 29° C.

The different concepts of preferred temperature have been thoroughly discussed by Gunn (Fraenkel & Gunn 1940, pp. 200-215), and we need only express our agreement with his view on the complexity of the phenomena and the shortcomings of the various methods of analyzing them. There is no doubt, however, that determinations of preferred temperature are useful in expressing the temperature reactions of poikilothermous animals.

Without entering further into a theoretical discussion we shall therefore simply state our definition of preferred temperature as the average of the temperatures at which the animals have come to rest under the given conditions. It is found by determining the point on the abscissa (Figure 1) where the S-shaped curve crosses the 50% ordinate. The present material on *Ascia* is insufficient to permit a determination of the function as a frequency distribution. It is more correct, therefore, not to indicate standard deviations and mean errors of the mean which would give an impression of statistical reliability which would most likely be an illusion.

Findings and Discussions

The experiments were carried out whenever the more important field work permitted and they consequently cover irregular periods of the year.

It was soon realized that the results varied considerably and that an analysis of these variations might well result in a better understanding of the ecological components of behavior. However, several variable factors were found during the final analysis of results which could easily have been better elucidated by further experiments had we had the opportunity to proceed with this work.

We have reason, then, to believe that several factors affect the preferred temperature. The difficulty in the analysis was to select such parts of the material in which only one of these factors varied while the others, as far as we know them, are kept constant.

Sex

In December 1949, after 13 experiments with 45 individuals, a preliminary analysis indicated no difference between males and females, so not much attention was paid to the sex of the butterflies in later experiments. In the final analysis, made some time later, comparison between sexes was made only in cases where both sexes had been caught simultaneously at the same place and had been treated in the same way. Nineteen such comparisons were found in the material, comprising 36 males (3763 observations) and 22 females (2601 observations). Only in 5 of the cases did the females prefer a higher temperature than the males. As a mean it was found that males pre-

ferred a temperature 0.8° C higher than the females.

A difference of 0.8° is not much compared with the individual variation in preferred temperature. It could, nevertheless, have some biological importance; field studies had revealed, for instance, that the females are usually the first to feed in the morning.

In the evaluations to follow no correction was made if the two sexes were present in the material in about equal numbers. In a few cases averages were obtained from observations involving exclusively one sex or nearly so; in such cases a correction of +0.4° is added if females predominated or —0.4° if males did.

Age

We have no evidence of any change in the preferred temperature during adult life. This could be because by far most butterflies were caught in the field and could thus have been of any age. In the 4 cases where newly-emerged individuals were tested they did not differ essentially from older individuals.

Hours since feeding

It became evident early in these studies that the preferred temperature rose during the day. For technical reasons we never started experiments until about noon and usually a little after noon. An experiment would often be in 2 parts, 2 to 4 hours of observation in the afternoon and then a similar period in the evening. All that time, the animals remained in the apparatus.

The very pronounced rise in preferred temperature from afternoon to evening could have 3 explanations: increase in age, time of day, or time since last feeding. The latter possibility was the easiest to investigate. In 7 cases determinations had been made simultaneously on individuals identical as far as we know except that some of them were fed a short time before the experiments while others had been without food for 24 hours or a little more. Butterflies from the field were usually caught while feeding and the hours since last feeding could be calculated from that moment. But when the final analysis showed how critical this period was we had to exclude several experiments because it was indicated only that the animals had been caught "in the morning."

If a meal had any influence on the preferred temperature, the effect was not likely to last over 24 hours. It was therefore assumed that butterflies which had fasted 24 hours had attained a preferred temperature value with which newly-fed individuals could be compared. In the 7 pairs of experiments involved, variation in preferred temperature in the animals which had not fed for 24 hours was small, 23.5° to 27.0°, the mean being 25.4°. In each pair of experiments listed in Table I corrections were made to bring all data in line with this mean. To the experimental values for short times since feeding was added or substracted whatever was needed to bring the matching 24-hour plus value to the mean of 25.4°.

TABLE I. Influence of a meal on the preferred temperature

Experiments	Hours since last meal	Number of Individuals	Number of Observations	Preferred Temperature	Corrected Temperature
30 - 45	2 - 3	2	106	28.4	28.3
	26 - 27	3	132	25.5	
	4 - 6	2	140	29.4	30.4
	29 - 31	2	140	24.4	
	7 - 9	2	134	25.8	24.6
	33 - 35	1	67	26.7	
166 - 175	1 - 4	3	270	26.1	25.7
	27 - 30	2	179	25.9	
	4 - 7	3	380	30.5	31.3
	30 - 33	2	256	24.6	
176 - 181	1 - 2	1	103	23.2	25.1
	24 - 26	2	204	23.5	
	4 - 6	1	73	30.0	28.4
	28 - 30	2	152	27.0	

The mean value of preferred temperature at each successive hour following feeding, based on the data of Table I, is shown in Figure 2. For the first hour after feeding the preferred temperature is the same as after 24 hours, but it then rises abruptly to a maximum 5 or 6 hours after the end of a meal. The 2 single (the others are averages) values at 8 and 9 hours are a little below normal (24.5° *vs.* 25.4°) but undoubtedly within the limits of normal variation. The drawn line is probably close to the true relationship between preferred temperature and time lapse since last feeding; it is used as a correction on all values of preferred temperature in what follows.

How this rise in preferred temperature should be interpreted is not clear. The natural food of the butterflies was nectar; in the laboratory they were fed honey water. Two male *Ascia* caught in the field in the morning were tested for preferred temperature in the afternoon. They were then kept overnight, one at 15% relative humidity and the other at 60-70% relative humidity, both at room temperatures (*ca.* 22°-23°), and tested again in the morning. The one from the humid chamber

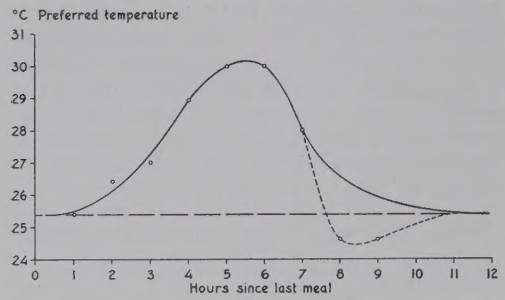

FIG. 2. Preferred temperatures after a meal. The broken line at 25.4° represents the "basic" value of the preferred temperature 24 hours or more after a meal.

kept its weight unchanged (121.5 mg) and showed an insignificant drop in preferred temperature, from 24.7° to 22.3°; we could not correct these values for time since feeding because this was unknown. The butterfly overnight in the dry chamber was somewhat desiccated, its weight having dropped from 87.0 to 83.5 mg. After the morning experiment both animals refused pure water but fed eagerly on honey water. The large one kept in the humid chamber increased its weight by 43% (121.5 to 176.0 mg); the desiccated one increased its weight by 46% (83.5 to 122.0 mg) or only slightly more. After the meal the rise in preferred temperature was not as much as usual, from 23.9° to 25.3° in one and from 22.3° to 24.7° in the other. The next day, both butterflies still exhibited rather high preferred temperatures, 25.4° and 26.0°. The meals in question were much larger than those usually given, however, and the abdomens were visibly inflated. During normal laboratory meals the butterflies were usually not permitted to feed more than 5 minutes whereas in the present experiment they fed for fully a half hour.

If anything can be deduced from the above experiment it is that (1) the rise in preferred temperature after meals is the result of food intake and is not related to water balance, and (2) after a very large meal the rise in preferred temperature is apparently delayed. In any attempt to explain these post-feeding changes it should be borne in mind that the rise in preferred temperature is not immediate and that the maximum is only attained after 5-6 hours.

Time of day

Although the rise in preferred temperature during the experimental day was demonstrated to be related to time elapsed since feeding, there still remained the possibility of a change in preferred temperature related purely to time of day.

For an analysis of this problem we selected all experiments which could be corrected for time since feeding and in which the same individual was tested more than once on the same day. In each pair of the 38 experiments so selected one of the observational periods was at 16^h. All preferred temperatures were then corrected to the mean value for this hour, 26.2°, and a mean calculated for each hour for which data were available, 12^h to 23^h. The results are presented in Figure 3. There seems to be a rise in preferred temperature in the late afternoon, about at the hour when daily activity for these butterflies normally ends. The rise is found to be about one degree, but it is so little pronounced that the only reason to mention it here is to call the attention to a possibility for further study.

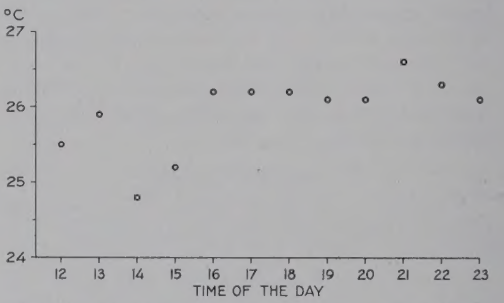

FIG. 3. Changes in preferred temperature according to time of day.

Time of the year

The experiments group themselves naturally into 4 periods:

(1) August 23-September 15 (20 exp.)
(2) October 8-November 1 (37 exp.)
(3) January 28-February 20 (43 exp.)
(4) March 21-April 19 (29 exp.)

For each of these 4 periods a mean was calculated for all determinations in which the time since feeding was known and an appropriate correction in preferred temperature made. The results are given as horizontal bars in Figure 4 and superimposed on a line representing mean air temperatures at Ft. Pierce through the year based on monthly means (U. S. Weather Bureau 1956).

It is unfortunate that we did not obtain sufficient microclimatic information to compare the seasonal changes in preferred temperature with temperatures in the *Batis* marshes and black mangrove areas where the development of *Ascia* occurs (Nielsen & Nielsen 1950, 1952). A detailed analysis of the relationship between environmental temperature and preferred temperature based upon meteorological means could hardly be justified;

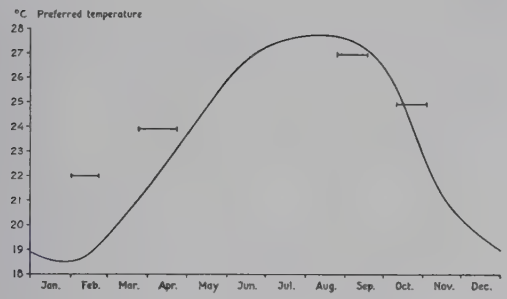

FIG. 4. Relationship of preferred temperature (shown as horizontal bars) to the seasonal change in air temperature at Ft. Pierce, Florida.

it is enough for now to state that there is a definite season change in preferred temperature correlated with the environmental temperature.

A few determinations were aimed directly at this problem. The first two such experiments were made in August when the room temperature was about 28°. There was no difference in preferred temperature between three males kept overnight at 20° and those kept at room temperature. Three fourth-instar larvae were kept at 20° and pupated at that temperature; the adults were tested when they emerged but did not differ from the normal temperature preference in that season. And, finally, 7 *Ascia* were brought from the field in April and kept at constant temperatures, 3 at 7°, 4 at 27°. Tested the next morning, their temperature preferences were found to be 22.3° and 22.8° respectively. It is unlikely therefore that the environment during the lifetime of the imago has any influence on its preferred temperature.

The seasonal temperature preference may thus be more likely to be imprinted early in the larval life than at a later developmental stage. It might be well at this juncture to recall that this butterfly exhibits another seasonal change; the typically white female becomes the dark-colored form *phileta* from March to October. However, females reared from eggs at 20° in August emerged as *phileta* and those reared at 28° in January developed into the typical white female for that time of year. It appears then that, although the color change is correlated with the seasons, it is not possible to produce it by manipulating the thermic element of the environment of the individuals, apparently leaving genetical factors to be involved.

A few experiments specially arranged showed no difference in temperature preferences between white and dark (*phileta*) females. No difference was found either between migrating and non-migrating individuals.

Larvae

The caterpillars of *Ascia* seem not to prefer any special temperature. Placed in the apparatus they moved in whichever direction their heads pointed to the end of the tube, where they usually stayed until paralyzed by cold or heat as the case may be. In the case of heat they usually died before they could be removed.

Pieris rapae

Ascia monuste occurs in Southern Florida and along the East coast; in North and West Florida it is replaced by *Pieris rapae*. The only case we found of both species occurring at the same locality was in Sebring in August, 1949. One male of each species was tested simultaneously. It is not possible from this single experiment to establish if the difference in preferred temperature was significant: *Ascia* 31.5°, *Pieris* 29.4°.

SUMMARY

By means of a technique described in detail, the temperatures preferred by *Ascia monuste* were investigated under a number of varied conditions.

(1) The preferred temperature is correlated with seasonal changes in temperature, with a difference of about 5° C between winter and summer.

(2) After a meal the temperature preference gradually rises to an elevation of nearly 4° some 5 to 6 hours later. This rise disappears at about 8 to 9 hours after the end of the meal.

(3) Males prefer a temperature about 0.8° higher than the females.

(4) There seems to be a possibility of a rise in the preferred temperature in the afternoon at the time when activity normally ends.

We have no proof of other factors having an important bearing on preferred temperature.

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OBSERVATIONS ON MOSQUITO POPULATIONS OF AN INTERMITTENT FOOTHILL STREAM IN CALIFORNIA

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Mosquitoes are well known from the west-slope foothills of the southern Sierra Nevada in California (Freeborn and Bohart 1951) but, as populations, are most notable for their unobtrusiveness. The small to moderate-sized streams which provide virtually all of the natural breeding sites in this zone are dry during the hot, rainless summer and so can be used effectively by mosquitoes only during the brief transition periods between that season and the cool-wet winter. The alternatives are for breeding to be carried on in winter waters which are flushed frequently by storms and in which temperatures average 10° C or less for months at a time or in the restricted and faunistically crowded bits of water that remain scattered along these watercourses through the summer. A general study (Abell 1956) of the seasonal development of the macrofauna in and around one such stream through 1953-1955 has yielded information on larval mosquito occurrence during the calendar year of 1954 that appears to be worth reporting separately at this time.

This work was conducted while the author was on a National Science Foundation Fellowship at the University of California, Berkeley. Special thanks are due to the California Department of Public Health, Bureau of Vector Control, for their generous loan of equipment and working space at their Fresno Field Station and to E. C. Loomis and H. F. Bormann, who critically read the manuscript.

DESCRIPTION OF HABITAT

Most of this study is concerned with a one-third mile section of Dry Creek in Fresno County, California. At this point the stream flows at an elevation of approximately 850 feet, through hills which are from 500 to 1500 feet higher and which are covered by the open-canopied oak-grassland community that is most characteristic of this zone. The willow-sycamore riparian community forms a rough line of trees along the stream which is only slightly less open than the surrounding oak-woodland.

Acting largely on my suggestion, Usinger (1956) has classified Dry Creek as a "long-flow fluctuating intermittent stream," for which this is the type example. I now prefer the term "extended-flow intermittent stream," as it is less cumbersome and seems to acknowledge the defining feature more appropriately, *viz.*, that the lower canyon reaches ordinarily begin flowing before the rainy season starts and continue for several weeks after the winter storms cease.

In the study area, Dry Creek discharges from one to four cubic feet per second during most of the 8-month flow season. Its bank-full volume of about 40 cubic feet per second is usually approached or exceeded several times each winter. The channel, which is largely free of vegetation, is made up of sandy pools interspersed between riffles in which well sorted, black-hued rubble-rocks and small boulders form the major bed types. This blackness results from the annual drying of the wet-season epilithon. The open riparian cover and uniform black hue of the stream-bed rocks are good indicators of intermittent conditions. In the mile and a half section of permanent flow 2 miles upstream, the riparian canopy is closed and is composed largely of alders, and the rocks are browner. Although most of the study area was completely dry it did contain a tiny permanent spring which sent a flow of a few gallons per minute 100 to 150 feet downstream and maintained, either by surface or subsurface flow, 7 pools during the summer of the study-year.

Mosquito habitat in and near the stream may be classified into the categories listed below. Descriptions of the types of habitat are included, supplementing the details given on the collecting stations in Table I.

I. Wet-season habitat:

A. Lateral pools.

True isolated lateral pools. This is the most important mosquito habitat-type associated with the stream. Seven such sites were present in the study area during 1954, all but one of which were important pools and/or backwaters in major, relatively high-threshold overflow channels of the stream. Because of their depth, the pools contained water throughout the flow-season (note exceptions IPF-1 and IPC-2 in Table I). Depth, proximity of riparian trees, and a rather high degree of sheltering from direct current in 5 of the pools favored the accumulation of organic debris, the decay of which caused the water to become darkly colored and covered with a thin

TABLE I. Summary of basic data on lateral pools and backwaters of Dry Creek in their 1954 form

Pool	Usual dimensions (feet)	Usual area (sq. ft.)	Usual max. depth (inches)	Cut-off threshhold* (feet)	Times flushed	Dry period	Shade	Collections	Special information
IPF-1	20 x 3	45	9	above 1.25	none	6/10-11/1	open	4/12-end	formed 3/29
IPF-2a	8 x 2½	18	9	0.82	6	6/20-11/1	open	all**	
IPF-2b	4 x 3	12	12	0.82	6	6/20-11/1	med.	all	
IPF-3	8 x 3	18	12	about 1.20	5	6/25-11/1	heavy	all	
IPF-4	3 x 1	3	7	above 3.00	none	6/ 8-11/11	med.	4/12-end	rock basin
IPC-1	6 x 4	20	24	about 2.00	3+2?	7/ 1-11/1	open	all	
IPC-2	5 x 3	12	15	0.93	2	7/11-11/ 1	open	4/12-end	formed 3/29
OP-1	Variable	about 2	1-3	0.80	8	frequent	med.	2/9-4/12	
OP-2	3 x 10	about 25	5	0.70?	7+	6/20-11/11	heavy	3/11-end	
OP-3	irreg.	about 50	6	0.75	6+?	5/12-12/10	med.	4/12, 5/4	
BW-1	3 x 2	4	1-3	0.40		5/30-11/14	med.	3/11 end[x]	often separated
BW-2	8 x 10	60	24	0.15		6/27-11/ 1	med.	6/4-end[x]	rarely separated
BW-3	7 x 2½	16	9	0.35		7/ 3-11/ 1	open	6/4-end[x]	usually connected
BW-4	2½ x 10	20	15	0.25		none	med.	5/4-end[x]	usually connected
OSP-1	30 x 10	225	18			6/30-11/ 1	med.	6/4-end[x]	
OSP-2	140 x 18	2000	30			7/ 1-11/ 1	open	5/4-end[x]	
OSP-3	60 x 10	500	30			9/14- 9/17?	heavy	6/4-11/16[x]	
OSP-4	25 x 8	300	20			none	open	5/4-end[x]	
OSP-5	110 x 15	1400	36			none	open	5/4-end[x]	

*Normal flow level at about 0.3-0.4 ft.; figures are averages of two staff-gauge measurements in the study area.
**"All" means that the full series of collections was made.
xUnder observation during preceding months when mosquitoes were almost completely absent from the mainstream proper.

oily film. Both of these features are indicative of anaerobic conditions. These were called *foul-type* pools. The other 2 pools (*clean-type*) apparently received sufficient subsurface seepage to keep the water at least moderately clean, discoloration and faint oily films appearing only during the longest of inter-storm periods. Most of the isolated lateral pools were situated beside boulders, bedrock outcrops, or root masses, all of which protected the pools from direct flow in all but the most severe of storms. Vegetation was scant or lacking in all of the pools except in May and June, when those which persisted became carpeted with algal blankets (largely *Hydrodictyon* and *Spirogyra*), duckweed (*Lemna*), *Nostoc* nodules, or water primrose (*Jussiaea*).

One pool (IPF-4 in Table I) was an exception in most of the above respects, being a rain-catchment basin created by stream erosion on a large outcrop of bedrock. Its season-long persistence and foul water (due to decay of a large quantity of sycamore leaves) placed it appropriately with the foul-type isolated lateral pools.

Overflow pools. The shorter, low-threshold overflow channels generally have a variety of small, shallow, short-lived pools which are greatly altered by each storm, receive little organic debris, and last only a few days after each surcharge period. Flushing is frequent and usually direct. While it lasts, the water ordinarily remains quite clean. Events were followed in 3 such sites. A few others were fleetingly present in the study area but were obviously of little significance.

B. Mainstream sites.

Backwater areas. Portions of mainstream pools are frequently more or less cut off from the current. Four such backwaters which appeared to be potential breeding sites for mosquitoes were selected for study. Each of these happened to be situated at the mouth of an overflow channel and was sheltered from the mainstream by a large mass of roots or solid rock. Depth, debris, vegetation, and storm-shelter conditions were all quite similar to those of true isolated lateral pools, but the water remained clean and the faunas were more varied because of the connection of these pools to the stream. All were directly flushed while the overflow channels (of moderate to high threshold) were flowing. Because these were sites in which separation from the current was extreme, lowering of discharge in late spring brought isolation and creation of typical isolated lateral pool conditions. Site BW-1 was dominated by emergent rushes but all the others were rapidly covered by *Nostoc* or *Lemna* carpets after isolation.

Pools of the open stream. The typical mainstream pool is a large, sand-bottomed depression which receives the full flow of the stream and has appreciable current through the center, except during periods of very low discharge, but contains considerable quiet water along the margins, where

flow-shelter created by roots, projecting rocks, embayments, or green vegetation (*e.g.* the semi-aquatic grass *Paspalum*) may persist even through severe storm flushings. Observations were made on 5 of the 19 such pools in the study area.

II. Summer habitat. Depressions in the stream bed, representing single or multiple pool sumps as well as scouring basins in riffles and slicks, usually contain water after general stream flow ceases. Most are temporary, but pools which last longer than 2 weeks often persist through all or nearly all of the summer. Thus, 2 classes are distinguishable. Some generalizations on mosquitoes are necessarily included in the descriptions, as follows:

A. *Temporary remnant pools.* (OSP-1, OSP-2 in Table I.) Conditions in the many bits of remnant water were extremely inconsistent. Plant and animal populations varied accordingly. Mosquitoes were noted wherever space was available at the surface, and the more active predators (e.g. Notonectidae and the fishes—*Lepomis cyanellus* and several native species of Cyprinidae) were lacking. Mosquitoes appeared to be densest in the clear, hot (27-34° C), shallow pools which occurred fleetingly in the most exposed sites (*e.g.* OSP-2).

B. *Persistent summer pools.* (OSP-3, 4, and 5 in Table I.) Each of the 7 permanent and semipermanent pools associated with the seepage spring in the study area contained a distinct aggregation of organisms, making generalizations difficult. Most pools did tend, however, to be dominated either by fish populations (when present) or by floating mats of vegetation, with the result that mosquitoes were largely excluded. Disruption of either form of domination favored mosquito populations. The larger and more stable pools retained diversified faunas in which mosquitoes appeared to have little place.

The Field Program

The collecting program was designed primarily to provide a simple description of the seasonal make-up of the mosquito fauna of this stream and secondarily to provide rough estimates of densities in the representative habitats.

Collections of immature mosquitoes were made with a one-pint dipper set on a 3-foot handle. A sample usually consisted of 6 dips, distributed in rough proportion to the area of each habitat variant (*e.g.* floating leaves, open water or emergent vegetation) within the pool. In small pools the number was sometimes limited by the disturbance of dipping and at larger sites more than 6 dips were often required to provide adequate coverage of the different types of habitat. Counts were made in the field, and a portion of each sample (at least 20 specimens if possible, some taken from each of 2 or more dips) was preserved in alcohol for identification in the laboratory. Most of the identifications were made by Miss Bettina Rosay, then of the California Mosquito Control Association, to whom special thanks are here extended.

A few collections of adult mosquitoes were made with a New Jersey-type light trap, using a 50-watt bulb, installed on the porch of a house one-quarter mile upstream from the upper end of the study area. It was situated 150 feet from the stream, just out of sight of the water.

Collections were made at approximate 28-day intervals throughout the calendar year of 1954 except that the August series was omitted because of illness. These collections were made as an adjunct to other field work; hence it was not possible to maintain a more precise schedule or to plan collections relative to the flushing of pools by storm surcharges.

The study began in January with collections from obvious sites of mosquito production. General field notes were taken on other situations in which populations were lacking. In February and March collections were made in 6 pools and detailed observations were recorded on 11 sites which showed promise as mosquito habitat but contained no larvae. From April on, actual dips were made as a matter of routine at 19 stations, including all of the earlier sites, whenever water was present on the collecting date. When expediency demanded, the note, "No mosquitoes present," was sometimes recorded for obviously uninhabited water even though no dips were actually made.

More than 2 years of observations on this stream indicated that these stations included practically all of the important sites of mosquito production in this one-third-mile section except for those involved in the brief bursts of more widespread reproduction associated with the resumption of flow in the fall and with the cessation of flow in the early summer. These periods are described in part by data from a few backwater and open-stream stations which were selected as representative of this much more extensive but usually unoccupied habitat.

Results

The results from the collections of immature mosquitoes are shown as density figures in Table II. Density is in the crude but widely used terms of "individuals per dip." The values for "all sites" in this table are "corrected" by counting each visual observation of "no mosquitoes present" at

TABLE II. Mosquito densities in the Dry Creek Study Area

Date	Jan. 12	Feb. 9	Mar. 11	Apr. 12	May 4	June 4	June 16	June 29	July 27	Sep. 22	Oct. 19	Nov. 16	Dec. 16
Isolated pools, foul													
No. of pools	3	3	3	5	5	5	1	dry				5	5
No. of dips	12	12	14	25	25	20	4					18	19
Density	12.8	38.0	28.4	13.1	33.1	20.0	4.5					67.9	49.6
Isolated pools, clean													
No. of pools	1	1	1	2	2	2	1	2	dry			2	2
No. of dips	6	7	12	20	12	12	2	5				12	9
Density	9.8	0	3.3	0.2	5.3	4.7	4.5	2.8				58.1	25.6
Overflow pools													
No. of pools		2	2	3	2	1	1		dry			2	1
No. of dips	obs.	4	11	23	12	6	1					6	6
Density	0	0	0	0	2.3	3.2	6.0					0	0
Backwaters													
No. of sites		4	4	4	1*	3	2	2	1	1	1	4	4
No. of dips	obs.	obs.	obs.	obs.	6	18	3	9	6	3	6	27	26
Density	0	0	0	0	0.5	9.8	7.0	24.2	52.2	0	8.3	9.8	0.1
Open stream pools													
No. of pools		5	5	5	2**	5	2	5	2	3	3	5	5
No. of dips	obs.	obs.	obs.	obs.	18	42	10	42	20	19	33	35	38
Density	0	0	0	0	0.5	0.6	0.1	2.6	5.2	4.6	13.6	5.9	0.1
All sites													
Corrected No. of sites	11	15	15	19	18	16	x	9	3	4	4	17	18
Corrected No. of dips	68	53	98	129	110	98	x	56	26	22	39	98	98
Over-all density	3.1	8.6	4.3	2.6	8.5	6.9	x	6.0	16.1	4.0	12.8	24.4	12.0

*This site isolated on this date; observations in three connected backwaters revealed no mosquitoes.
**No mosquitoes noted in observations on the other three pools in the regular series.
"Obs." indicates that observations were made but no collections were taken.

any of the regular sites as 6 dips, each yielding no catch. Data are included in this table for a series of collections on June 16 which was considered inadequate for an accurate over-all density figure. Density values are not listed for the entire year in each habitat type because the comparisons thus suggested would be misleading if not directly associated with explanations. However, the year's density figures for the three types of lateral pools (foul type, 38.2 mosquitoes per dip; clean type, 12.1; overflow pools, 0.8) can be compared fairly reliably since the data cover the same period for each type. Also, these stations did not undergo drastic environmental changes during the year.

Conversely, backwater and open-stream sites were each converted to very different types of habitat and for different lengths of time as the intermittent period approached. Thus, the backwater sites had a mean density of 5.4 mosquitoes per dip while they were connected and of 15.4 while isolated from the stream. Similarly, density averaged 1.1 mosquitoes per dip in the pools of the open stream and 5.7 during the intermittent period. As noted in the preceding sections, the figures for lateral pools include nearly all available sites, whereas the mainstream stations must be regarded as "selectively representative."

The figures on species composition, stated as percentages in Table III, show *Culiseta incidens* to have been the winter mosquito during 1954 and *Anopheles franciscanus* to have out-numbered all other species (mostly *Culex*) during midsummer. Most of the specimens designated "*Culiseta* spp." and "*Anopheles* spp." were early instars or pupae of these same species. Other species of these genera were present at approximately the same time but in much lower numbers.

Species of each of the 3 genera are lumped in Figure 1 to show percentage composition of the mosquito fauna through the year. The several species of *Culex* can be seen to have reached their peak in a short period between the drop-off of *Culiseta* and the midsummer rise of *Anopheles*.

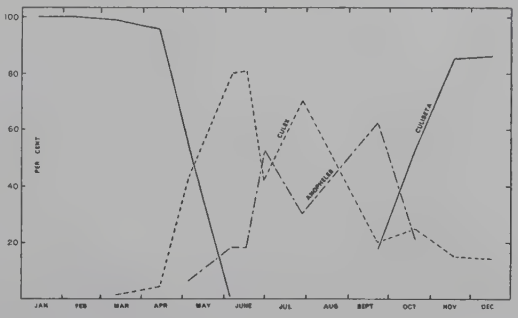

FIG. 1. Composition of the mosquito fauna of Dry Creek during 1954.

The midsummer peak of *Culex* is probably erroneous, the figure shown here being quite in conflict with general observations made over a wider

TABLE III. Species composition of preserved collections (stated in % except as noted)

Species	Jan. 12	Feb. 9	Mar. 11	Apr. 12	May 4	June 4	June 29	July 27	Sep. 22	Oct. 19	Nov. 16	Dec. 16	Total Counts	Per cent
	%	%	%	%	%	%	%	%	%	%	%	%		%
Anopheles freeborni (Aitken)					0.4								1	
A. franciscanus (McCracken)						0.7	19.4	3.7	36.7	6.0			53	2.1
A. punctipennis (Say)							1.6			0.7			3	0.1
Anopheles spp. (unidentified)					2.2	10.8	13.7	22.4	3.3				107	4.3
Culiseta incidens (Thomp.)	22.1	63.3	92.8	89.7	43.9					42.5	66.4	54.0	1097	43.7
C. inornata (Williston)												5.9	20	0.8
Culiseta spp. (unidentified)	77.9	36.7	5.7	6.2	14.6	0.3			6.7?	24.6?	22.1	25.8	434	17.3
Culex apicalis (Adams)				2.1	11.5	8.1	4.0	17.5	36.7	3.7	0.4		126	5.0
C. boharti (Brookman & Reeves)						0.3							1	
C. quinquefasciatus (Say)											0.4	2.9	12	0.5
C. restuans (Theobald)												4.4	15	0.6
C. stigmatosoma (Dyar)					2.8	17.2	12.1	1.3	3.3	3.0	5.4	2.9	119	4.7
C. tarsalis (Coquillett)				1.4	15.0	5.4	9.7	0.9					80	3.2
C. thriambus (Dyar)			1.4		3.7	12.1	9.7	19.7	13.3	14.9	4.6	2.6	161	6.4
Culex spp. (unidentified)				0.7	5.9	45.1	29.8	34.5		4.5	0.6	1.5	282	11.2
Total counts	95	180	141	146	321	297	124	223	30	134	479	341	2511	99.9

area and longer period of time. On this date it happened that the collections for identification were taken from only 3 sites and a disproportionately large number of specimens was included from a small, decay-dominated pool (BW-5) in which an unusually dense population of *Culex* was present. It should also be noted that a very real rise in the importance of *Culex* in November is obscured by the massive reentry of *Culiseta* into the fauna.

An analysis of the occurrence of the various species of *Culex* (Table III) shows *Culex thriambus* to be the most numerous, but only slightly more so than *C. apicalis* and *C. stigmatosoma*. Totals of *C. tarsalis* for the year were slightly lower, primarily because its season apparently did not extend beyond July. Inspection of the raw data (not included here) suggests a preference on the part of all species of *Culex* for the foulest of sites, with the one added note that *C. stigmatosoma* was apparently able to use the clean water of the open stream in the November population surge much more readily than the other species of the genus.

TABLE IV. Light-trap collections of adult mosquitoes one-quarter mile from the study area

Species	June 26-July 30 (13 nights)	October 16-November 11 (10 nights)
Anopheles punctipennis	1	
A. franciscanus	117	20
Aedes melanimon	1	
A. nigromaculus	1	
Culiseta incidens		14
C. inornata	1	25
Orthopodomyia californica	1	
Culex apicalis		2
C. stigmatosoma	9	12
C. tarsalis	13	24
C. thriambus	2	3

The light-trap captures are shown in Table IV. Unexpected features are: (1) the occurrence of two species of *Aedes—A. melanimon* Dyar and *A. nigromaculus* (Ludlow)—in the vicinity of the stream; (2) the predominance of *Culiseta inornata,* a common species in the nearby San Joaquin Valley, over *C. incidens* in the light-trap material; and (3) the low numbers of *Culex apicalis* and *C. thriambus* in the trap. *Orthopodomyia californica* R. Bohart is a tree-hole species (Reeves 1941).

DISCUSSION

If this stream and this year can be regarded as typical, it is evident that larval mosquitoes are present in association with the extended-flow type of intermittent stream throughout the year. Their occurrence is diagrammed in Figure 2.

During most of the flow season, mosquito populations are almost entirely restricted to isolated lateral pools, particularly the foulest ones. Hence, the total population of immature mosquitoes during most of the year depends upon the number of such sites present. Few of these streams appear to have more than a dozen or so isolated lateral pools per mile, so it seems fairly safe to say that streams of this type cannot ordinarily produce great numbers of mosquitoes.

As water levels recede with the slackening of

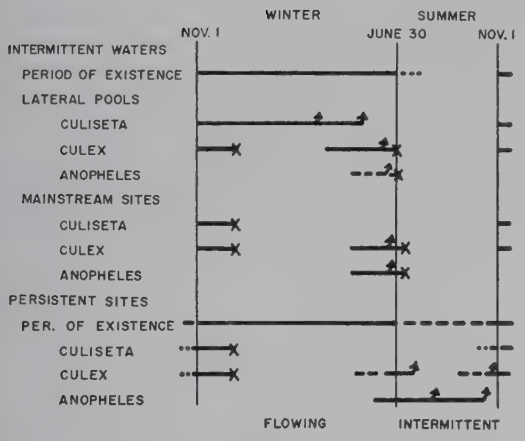

FIG. 2. Phenologic diagram of Dry Creek mosquitoes. Upward arrows indicate presumed emergences; x-marks, probable destruction of the population of immatures; dashed lines, weak occurrence.

storms and increase of temperature in the spring, the factor of periodic flushing is more or less eliminated and conditions in the isolated lateral pools become somewhat less difficult for immature mosquitoes. At the same time, backwaters of mainstream pools are being cut off entirely from the stream to become typical isolated lateral pools. But, as rapidly as flushing recedes in importance and the number of lateral pools is increased, the resulting tendencies for mosquito reproduction to be more successful are usually offset by the development of several unfavorable influences. One is the fairly rapid decrease in size of the pools as the streams continue to recede. Another is the frequent invasion of these pools by scavengers and predators—most of them air-breathers, including several hydrophilid and dytiscid beetles and aquatic Hemiptera. A third such influence is the domination of many of the pool surfaces by floating vegetation. Although waves of production, first of *Culiseta* and then the several species of *Culex*, may occur in some pools, the total population of immature mosquitoes is probably not increased as the stream dwindles.

As has already been mentioned, cessation of general stream flow (often associated with a sudden hot spell in early summer, when virtually all of the extended-flow section will fail at once) leaves many bits of remnant water. Depending, apparently, upon what other animals happen to be stranded there, many of these pools harbor mosquito populations for as long as the water lasts, but the obvious loss of a large portion of the total population as the pools quickly dry would seem to militate against any great amount of production of adults.

During midsummer, mosquitoes are restricted to the scattered, permanent, stream-bed pools, in which they usually fare rather poorly. Exceptions are the occurrence of low numbers of *Anopheles* in cup-like depressions in the algal blankets of some clean-water pools and occasional larger numbers of *Culex* in pools in which the oxygen balance is upset by bacterial decay. Situations in which either of these special conditions occur are not common in these streams during the long, dry summer season. One or 2 small clusters of pools per mile, similar to those observed in the Dry Creek study area, would be a reasonable average in most such watercourses. Probably less than one-fifth of them will offer the necessary conditions for mosquito production.

During the fall virtually the entire stream is populated by mosquito larvae. Down-canyon from the permanent-flow section, the several miles of rejuvenated and virtually unoccupied stream are rapidly invaded by large numbers of larval *Culiseta incidens* and *Culex stigmatosoma* (plus a few *C. apicalis* and *C. thriambus*). If temperatures stay up and storms are not immediately forthcoming, large numbers of adult mosquitoes may emerge. Ordinarily, however, the bulk of these mainstream mosquitoes are flushed out by an early storm and presumably destroyed. There is apparently little place for mosquitoes after this in the rapidly developing mainstream fauna, and the winter situation, with mosquitoes tenuously occupying the isolated lateral pools only, is thereupon reëstablished.

Figure 2 is a schematization of this entire picture. This diagram, based on the data presented in Table V, is speculative insofar as the fate of the mosquitoes (marked by upward arrows indicating emergence and x's indicating destruction) is concerned. Some suggestion as to the relative numbers involved may be drawn from the figures listed in the table. Here the importance of the foul-type intermittent lateral pools may easily be seen. In addition, *Anopheles* appears to be associated almost entirely with the clean mainstream pools, whereas the foul isolated summer pool was occupied largely by *Culex* species.

Some interpretation and explanation of the results of this work, referable to the generalized case, also seem to be in order. First why are mosquitoes unable to reinvade the mainstream after the first fall flushing? Higher temperatures, a fairly stable food supply, and generally adequate shelter from the occasional flushings due to storms obviously make the lateral pools good habitat. However, these factors are only slightly less favorable in the better backwater sites on the main-

TABLE V. Numbers of mosquitoes taken from the different types of habitat in 1954

	DATE OF COLLECTION												Year Total	%
	1/12	2/9	3/11	4/12	5/4	6/4	6/29	7/27	9/22	10/19	11/16	12/16		
Intermittent lateral pools	(3)	(2)	(3)	(5)	(6)	(7)	(2)	dry			(5)	(5)	(38)	
Anopheles	0	0	0	0	1	17	1				0	0	19	1.1
Culiseta	95	180	139	140	188	1	0				328	298	1369	78.3
Culex	0	0	0	6	108	165	5				30	47	361	20.6
Intermittent mainstream pools	(1)	no collections			(2)	(3)	(4)	dry			(1)	(0)	(11)	
Anopheles	0				6	6	37				0		49	29.7
Culiseta	17				0	0	0				29		46	27.9
Culex	0				8	8	22				32		70	42.4
Persistent mainstream pools	no collections					(4)	(3)	(2)	(3)	(3)	(1)	(0)	(16)	
Anopheles						29	70	57	49	26	0		231	61.3
Culiseta						0	0	0	14	54	18		86	22.8
Culex						11	2	2	16	24	5		60	15.9
Persistent backwater (isolated)	connected					(1)	(1)	(1)	obs.	(1)	connected		(4)	
Anopheles						1	0	1	0	0			2	0.8
Culiseta						0	0	0	0	21			21	8.4
Culex						35	53	133	0	6			227	90.7

*Figures in parentheses indicate number of sites sampled. All other figures to the left of the "Per Cent" column are numbers of individuals retained and identified.

stream. The major difference between the 2 types of habitat seems to be the accessibility of the backwaters for some of the large and active predators of the mainstream fauna, and it is to these animals that we can probably assign much of the responsibility for keeping these waters free of mosquitoes. Adults and larvae of the predaceous diving beetle *Agabus* are common in the fall stream but rarely in the lateral pools. The same is true for adult Notonectidae. Depredation by these insects must certainly be of some significance. An adult *Notonecta kirbyi* quickly killed several *Culiseta* larvae in a collecting jar on one occasion, and in another instance (May 5, 1954) approximately 20 adult *Agabus* sp. were seen swimming in an isolated lateral pool that had been heavily populated with culicine larvae only 3 days before but which was now devoid of mosquitoes. This was actually a rather unusual event since *Agabus* is rarely encountered away from the flowing stream.

The adaptation of *Culiseta* to the harsh conditions of the winter stream is worthy of some mention. In the late fall, both *Culex* and *Culiseta* are present in the lateral pools. Time and presumably several flushings soon bring the elimination of *Culex* but the few *Culiseta* larvae which manage to keep their positions in the storm-swept pools are joined in all but the very coldest portions of the winter by new, freshly hatched individuals. A period of balmy, stormless weather may then bring a notable build-up in these pools. The predominence of fourth instar larvae in many collections suggests a regular developmental delay at this stage, however, and casts some doubt upon the effectiveness of this mid-winter reproduction. A delay of this sort would greatly lower the chances for completion of the life cycle. Additional investigation might well be directed toward the comparative emergence-success of winter versus spring generations of *Culiseta*. The replacement of *Culiseta* by *Culex* in the late spring does not mean, however, that the former genus is limited to cold-weather reproduction, for the first larvae appear in late summer, when air temperatures may still frequently approach 38° C. The advance of general stream flow into this area from the permanent section is preceded by a general rise in subsurface water levels, refilling some stream-bed pools and raising levels in persistent ones so that a moat of open water appears at the edge of pools where heavy carpets of floating vegetation have greatly restricted the fauna. Such water soon supports vigorous populations of both *Culex* and *Culiseta*.

The problem of defining the general role of mosquitoes in a stream such as this merits some attention also. The Dry Creek Study suggests that mosquitoes occupy two ecologic positions in the extended-flow type of intermittent stream. Most importantly, they are members of the pioneer animal association in new and disturbed habitats. Thus, mosquitoes occur (1) in the entire rejuvenated stream in the fall, (2) in the regularly flushed lateral pools throughout the winter, (3) in the separated stream-bed pools when flow ceases in the early summer (this being "new" habitat in the sense that the dominating influence of current is now completely removed), (4) in breaks in the faunally restrictive *Azolla* carpet of clean, midsummer pools, and (5) in separated pools that

appear in the stream-bed in late summer as ground water levels rise prior to the resumption of flow. This may be called the "opportunistic" role of mosquitoes in the intermittent stream environment. The term appears applicable to all 3 genera occurring in this stream, although it must be noted that *Anopheles* is considerably less adept in this way, its obvious pioneering role being limited to occupancy of the warmer, shallower pools which remain as temporary remnants in the stream channel.

The other position may be called the "continuing" one. In this role, mosquitoes are occupants of special habitats in which the fauna is greatly restricted by biotic factors. Thus, *Culiseta* and probably most species of *Culex* occur as occupants of separated pools in which the diversified clean-water fauna is absent, apparently because of the decay of relatively large quantities of organic matter (usually leaf material). The continuing role of *Anopheles* is in cup-like depressions in floating mats of *Spirogyra* and *Hydrodictyon*. One rarely finds any animals but *Anopheles* in such sites. Most other animals that might enter from the terrestrial-aerial environment seem to require access to the substrate. Entrance from the pool below seems to be barred by the algal blanket, which is, itself, faunally depauperate.

The ecological versatility shown by such mosquitoes as *Culiseta incidens* and *Culex thriambus* in occupying, with equal ease, the foulest of isolated pools and the clean waters of the freshly rejuvenated stream is difficult to understand. Perhaps the "continuing" (foul-water) habitats could be interpreted as sustained disturbance situations in which the animal associations never proceed past the pioneer stage, in which culicenes are the most conspicuous members. Supporting this suggestion is the observation that the persistent backwater listed at the bottom of Table IV fostered a *Culex* population through June and July, while foul water conditions obtained, but, when its oxygen balance was restored in September in apparent association with the development of a partial surface carpet of *Lemna*, the mosquitoes disappeared.

There is no easy explanation for the absence of *Aedes* in this stream, and, as far as I can see, apparently from this type of water. Despite the presence of adult *Aedes* in the area (Table V) larvae were not taken in the stream either in the mosquito work or in the broader study which included collections from most of the length of Dry Creek and from 10 similar streams from Mariposa to southern Tulare counties.

Summary

1. Dipper collections of immature mosquitoes were taken at monthly intervals during a single calendar year from water associated with an extended-flow-type intermittent stream in the western foothills of the Sierra Nevada in central California.

2. Mosquito larvae were present along the stream throughout the year but during most of the 8-month flow-season were largely restricted to isolated lateral pools and during the summer dry season to certain of the scattered permanent pools in the main channel.

3. Mosquitoes invaded all quiet-water habitat in and around the stream in great numbers in the first days after flow resumed in the fall (by steady progression downstream from a short section of permanent flow at the 1000-foot elevation) and remained until emergence or until the stream was flushed out by the first rains in mid-November.

4. A less significant population expansion came when stream flow ceased in June, leaving many scattered remnant pools as temporary habitat. This expansion followed a gradual increase in lateral pool populations during the progressively warmer and more storm-free spring period.

5. Winter populations were made up almost entirely of *Culiseta incidens*, whereas *Anopheles franciscanus* tended to make most effective use of the summer pools. Several species of *Culex* dominated the spring scene and joined *Culiseta* in the invasion of the new stream in the fall, after continuing through the summer in the fouler of stream-bed pools.

6. It is suggested that mosquitoes fill two general ecologic roles in this type of stream: (a) an opportunistic role in which they are among the first invaders of disturbed and new habitat, and (b) a continuing role in which they are regular residents in such specialized habitats as isolated lateral pools that are completely dominated by decay and cup-like depressions on the surface of floating algal blankets.

7. Adult mosquitoes of the genus *Aedes* were taken in light-traps near the study area but the larvae were never encountered in the stream.

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THE RELATIONSHIP OF PRECIPITATION AND BLACK-TAILED JACK RABBIT POPULATIONS IN KANSAS[1]

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Populations of black-tailed jack rabbits (*Lepus californicus ssp.*) have increased to near plague proportions at various times in many western states. The limited records show that western Kansas has experienced two population increases of such proportions and that both have occurred during droughts (Wooster 1935, Carter 1939, Bronson 1957). The subspecies present in this region is *L. c. melanotis*.

The economy of western Kansas is principally agricultural and, when large numbers of these animals are present, excessive crop damage may result. Reports of crop damage in 1954-'55 and 1955-'56 reached proportions unheard of since the drought of the mid-1930's. "Rabbit drives," common methods of destruction in the 1930's, were held again in many western counties. Unconfirmed reports stated that as many as a thousand or more jack rabbits were killed on some of these drives.

A study of the ecology of this hare, its population fluctuations, reproduction, habits and economic effects was begun in July of 1956 and is continuing. This paper presents data on the changes in the number of jack rabbits on a study area in relation to the termination of a five-year drought (1952-1956). The possible relation between the data collected on the study area and the long-term population fluctuations of this species in Kansas is explored. Thorough studies of the ecology of *L. californicus ssp.* have been made in Arizona by Vorhies and Taylor (1933) and in California by Lechleitner (1956). Woodbury (1955) charted an annual cycle of these animals in Utah.

STUDY AREA

Studies were conducted in the Arkansas River valley in eastern Kearny County and in the sand-hills lying to the south of the valley. This range of sand-hills extends from southeastern Colorado eastward through 5 Kansas counties and varies in width up to 20 miles. The soils are sandy with some small areas denuded of vegetation. The sand-hill area was originally a post-climax mid-grass region where the dominant grass was little bluestem (*Andropogon scoparius*). Overgrazing and drought conditions have caused secondary succession in most of the region. The principal plants on the study area were red threeawn (*Aristida longiseta*), buffalograss (*Buchloe dactyloides*), russian thistle (*Salsola kali*), and sand sagebrush (*Artemisia filifolia*). Scientific names of the plants follow Harrington (1954). The Arkansas River valley is an intensively farmed region where irrigation is heavily relied upon as an agricultural aid. The principal crops were hard winter wheat, grain sorghum and alfalfa. The average annual rainfall is 16.8 inches with most coming during the spring and early summer months. The precipitation totaled 7.5 inches in 1956, 21.9 in the first 11 months of 1957, with an annual average of 11.2 inches during the five-year drought.

Most of the jack rabbits were found in the sand-hill pastures during the daytime hours. Many animals in the pastures adjacent to the river valley displayed a definite daily movement pattern. This consisted of an evening movement of animals north into the croplands to feed intermittently throughout the night followed by the return at sunrise to the pastures which served as their daytime resting area. It was determined from the amount of crop damage in different fields that the jack rabbits usually moved into the river valley only as far as the nearest food sources on their nocturnal foraging trips. Illustrative of the magnitude of the evening movement was a high count of 126 (31 possible repeats) jack rabbits crossing into the cropland from the sand-hills on 0.7 mile of road in one hour.

Population studies were conducted on two areas totaling 2240 acres. One area, named the primary study area (1920 acres), was located across an ecotone and consisted of about 70% sand-hill pasture land and 30% river valley cropland (Figure 1). Data from this area were obtained during the entire 17 month study period. The other area, called the secondary study area (320 acres), was located one mile farther into the hills than the primary area and was studied only during the last 8 months of the study. It was assumed that the primary area was representative

[1] This is contribution Number 284 from the Kansas Agricultural Experiment Station in the Department of Zoology; and number 324 from the Department of Zoology. Assistance was received from the U. S. Public Health Service and the Kansas Forestry, Fish and Game Commission. The authors wish to thank Dr. R. R. Lechleitner, Fort Collins, Colorado for the use of a manuscript.

of the cropland-edge of hills ecotone and that the secondary area was representative of the more interior region of the sand-hills. Population trends were established for these areas by using a variation of the strip census method. The primary study area was first subdivided into 320- or 640-acre divisions and 100-foot wide flushing strips were established at one-fourth mile intervals on each of these subdivisions. The strips extended the entire length of each division resulting in a sampling intensity of 8%. A direct count of animals on this 8% of each subdivision comprised the index of abundance for that subdivision for each indexing period. A similar procedure was followed on the secondary area. The observer walked fixed paths down the center of each strip while obtaining the direct counts. The short grass-sagebrush type of cover, and the fact that the animals rest in conspicuous forms, made an ideal situation for this type of direct counting. The total length of all counting strips was 12 miles during the first 4 indexing periods and 14 miles during the last 3 periods.

Data on the distances from the observer at which jack rabbits flushed were recorded in April and June of 1957 to determine if an area of 50 feet on either side of a line was too wide a strip and to determine the effect of the varying amount of vegetation on flushing distances. Analyses of these data indicated that a strip 100 feet wide was within the limits of accuracy for the vegetation types in which it was employed. Several conditions under which counts for indices were to be made were established at the beginning of the study in an attempt to make all indexing periods as environmentally comparable as possible. Counts were made only between the hours of 10 a.m. and 3 p.m. because jack rabbits are normally inactive during those hours. Indexing was done only when weather was normal, that is, wind at a minimum, no rain or snow falling, the ground relatively dry, and the temperature within the normal range for the season. In addition to data from the study areas, hunting success and field observations yielded data on population trends in northern Kearny County.

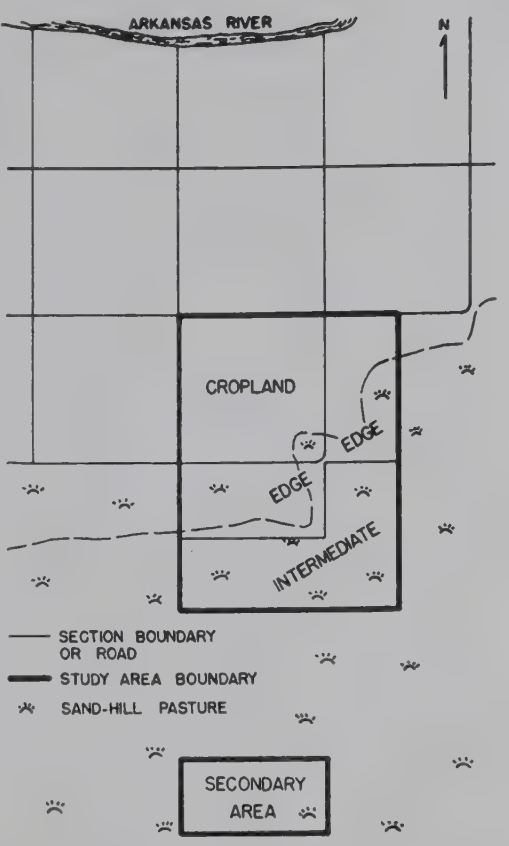

FIG. 1. Region where population studies were conducted.

RESULTS

The change in numbers of animals on the primary study area revealed a pattern completely unlike the pattern shown by a normal, stable prey population (Figure 2). In terms of the annual reproductive cycle of the jack rabbit, a stable population would have been expected to increase until September, 1956 (one month after breeding ceased) and then decrease sharply during the non-breeding season. The number of animals should have increased again after reproduction began in February and then have decreased after September of 1957. The number of animals, as indicated by the indices of abundance, decreased by only 20% during the 8 month period of September, 1956 through April, 1957. Since 8% of the study area was sampled and, assuming that the indexing strips were representative of the area, this drop of 20% would represent about 170 animals. The total mortality on the area was undetermined but was exceptionally heavy. Known predator, road and landowner kills totaled 186 animals for this 8-month period. Market hunting for bounty and carcass payments was also exceptionally heavy. As many as 6 parties of hunters in automobiles were observed on or near the primary area during a single night. It is apparent that during the fall and winter months, many more animals were killed on the area than the results of comparing the indices of abundance revealed. The reason for this failure to decrease greatly in numbers, even though mortality was heavy, was immigration into

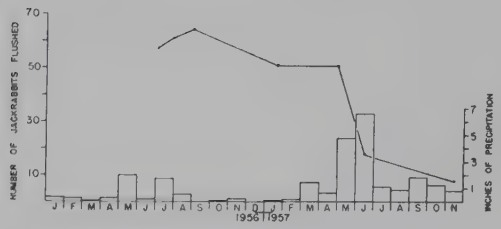

FIG. 2. Number of jack rabbits flushed on counting strips of primary study are (dot and line) and monthly precipitation (histogram).

the area. Dispersion of these animals resulted in a sharp drop in May, 1957 (Figure 2).

Changes in the amount of natural food available was the primary factor in causing variations in the abundance of jack rabbits on the study area. Soil moisture is the limiting factor for plant growth in southwestern Kansas. The sand-hills had been subjected to almost constant drought conditions since 1952 and the vegetational cover in these hills had been badly damaged by drought and overgrazing. Total rainfall in May of 1956 was near average but individually the rains were of small amount and resulted in only a limited growth of forbs and grasses in the sand-hills. Overgrazing and drought caused this natural food supply to be exhausted. This failure caused jack rabbits to concentrate in low areas where some food remained or along the periphery of the sand-hills where food was available to them on their nightly foraging trips into the croplands. The almost complete loss of natural food during the winter caused all animals to move out of the center of the hills and to concentrate along the edges near cultivated crops. The concentration of animals on the primary area dispersed when heavy rains in the spring of 1957 again provided a plentiful food supply in the hills. The inverse relationship between the amounts of rainfall and the number of jack rabbits is noted in Figure 2.

Further evidence of the concentration and dispersion movements is found in the variation between the number of animals flushed on the various subdivisions of the primary study area and on the secondary area. The divisions of the primary study area were aggregated and named as follows: (1) the 640-acre region in the river valley was called the "cropland"; (2) the 640 acres lying along the edge of the hills was called the "edge"; and (3) the 640 acres interior to the "edge" was named the "intermediate" section (Figure 1). The "edge," "intermediate" and the secondary area, therefore, were of the same general cover type but differed only in location in the sand-hills. The changes in the abundance of animals on these divisions are noted in Figure 3. The 20% drop in population abundance that occurred during the 8-month period of September 1956 through April 1957 was accounted for by losses in the "intermediate" area while the number of jack rabbits in the "edge" section remained high because of continued immigration. The effect of spring rains in 1957 and the subsequent dispersion movements are evident. The secondary area was first censused in April, 1957; however, observation trips into the area during the winter of 1956-'57 revealed that few, if any, animals were present.

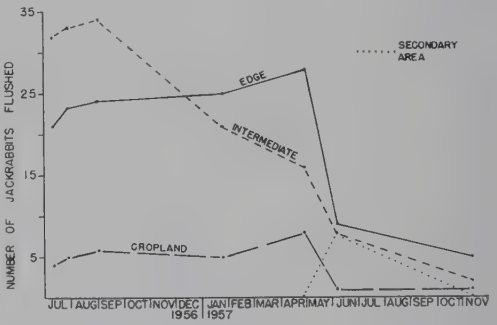

FIG. 3. Number of jack rabbits flushed on the counting strips of primary study area divisions and secondary study area.

As the dispersion occurred in May and June, the number of animals flushed per mile of censusing strips became approximately the same as in the other sand-hill regions.

If a direct count of 8% of an area can be considered an adequate sample and, assuming that the flushing strips were representative of the area, then population density estimates may be made (Table 1). For that stage of the population fluctuation which occurred in 1957, a normal (when food was available) density in the sand-hill pastures was about one jack rabbit per 4 to 6 acres. When food was not available and the jack rabbits were forced to concentrate near a food source, recorded daytime densities reached one per 1.4 acre, despite heavy mortality. The daytime population densities recorded on the cropland area varied from one jack rabbit for every 10 acres to about one for every 50 acres. In an effort to determine the densities on the cropland when the concentrations of jack rabbits moved out of the hills to feed at night, nocturnal feeding counts were conducted on specific crop fields. The highest count made on larger fields was 203 animals (14 per acre) on a 14.5 acre wheat field during the winter of 1956-'57.

TABLE 1. Density estimates (jackrabbits/acre) based on expanded indices of abundance

Indexing period	"Cropland"	"Edge"	"Intermediate"	Secondary Area
July (early) '56	0.1	0.4	0.7	
July (late)	0.1	0.5	0.7	
September	0.1	0.5	0.7	
January '57	0.1	0.5	0.4	
April	0.2	0.6	0.3	0.0
June	0.1	0.2	0.2	0.2
November	0.0	0.1	0.0	0.0

DISCUSSION

During the course of a 17-month investigation of these hares, certain factors which affect jack rabbit populations became apparent. From the data collected, certain inferences may be made and applied toward an understanding of the long-term changes in numbers. By studying data gathered from farmers, county agents and fish and game personnel the apparent history of the increase that occurred during the 1952-'56 drought was established. A noticeable increase in the number of jack rabbits in many areas of western Kansas occurred in 1953. The amount of crop damage in the period 1954 through 1956 was reminiscent of that which occurred in the 1930's. In the fall of 1957, the population was believed to have stabilized.

From the evidence available in publications these animals are not cyclic in Kansas but rather increase markedly only during dry periods. There have been two droughts of consequence in Kansas since 1930. The first occurred during the mid-1930's when Wooster (1935) wrote: ". . . the black-tailed jack rabbit has shown marked increase in the winter of the second of two dry years and in the following dry, hot summers." The data from this study would seem to indicate that the apparent population increase which took place during the 1952-'56 drought was in reality only a concentration of the population. It is the authors' opinion that the number of jack rabbits in large regions of western Kansas did increase during the initial part of the drought period. However, it is felt that the apparent jack rabbit population fluctuation was as much, or more, a function of concentration and dispersion movements as of an actual increase or decrease in numbers. In most instances, the animals concentrated near food sources as on the study area located along the edge of the sand-hills. However, in the flat lands north of the Arkansas River valley, jack rabbits concentrated in brushy draws or wheat stubble fields because these were the only available habitats suitable for daytime resting areas. The jack rabbits left these resting areas at night to feed on the surrounding croplands in the same type of movement, only on a smaller scale, as the daily movement pattern of the animals concentrated along the edge of the sand-hills.

The work of Vorhies and Taylor (1933) and Vorhies (1936) may have application in population increases in Kansas. They found that overgrazing, unless too severe, created a more favorable habitat for jack rabbits. Taylor and Lay (1944) were of the opinion that jack rabbits increase in numbers as overgrazing removes the grasses. It would seem, therefore, that drought and overgrazing are factors which may increase the carrying capacity of an area for jack rabbits by altering the vegetation. Some support for this hypothesis was in evidence from hunting success and censusing data. The over-all vegetational cover of the sand-hills became progressively more dense as the relatively heavy rains continued through 1957. Specimens were as readily collected along some of the brushy draws north of the Arkansas River as they had been in 1956. Apparently, as the drought ended, the density of the vegetation was affected differently in various areas and the number of jack rabbits was also variously affected. In areas where the increased rainfall caused revegetation by a dense stand of weeds and grasses, the carrying capacity for jack rabbits was decreased. The continued decline of jack rabbits on the primary study area after the dispersion movements in the spring of 1957 was probably caused by such an increase in vegetation.

The recent drought may then have had a two-fold effect on the numbers of jack rabbits. As the amount of vegetation was altered (reduced) in pasture areas such as the sand-hills during the initial part of the drought period, the carrying capacity on those areas was increased. As the drought continued, the regions which became denuded could not support the larger populations, particularly during the winter months, and the animals were forced to concentrate in smaller areas to obtain food and/or suitable habitat for daytime resting areas. These concentrations resulted in locally heavy crop damage and reports of "hundreds of jack rabbits per square mile" often reported in Kansas during the recent drought.

Some comments on population movements are pertinent. Concentration and dispersion movements have been recorded for other animals. Usually these movements have been dependent upon the food supply. If the only records available for the jack rabbit study area had been counts (or indices) of animals, the population trend (Figure 2) would probably have been interpreted as a definite decrease in numbers in the population.

This may be an important variable in populations studies. Similar movements in other populations could be interpreted to indicate actual population fluctuations, particularly where only censusing data from a small study area are available.

Summary

Data are presented on the changes in numbers of black-tailed jack rabbits on a study area in relation to the termination of a 5-year drought. The data were collected during the period July, 1956 to November, 1957 in the Arkansas River valley and the sand-hills of east-central Kearny County, Kansas.

An inverse relationship between the monthly precipitation and the abundance of jack rabbits was indicated for the study area located in the edge of the sand-hill region. When drought and overgrazing depleted the food supply in the hills, the jack rabbits migrated to the edge of the hills in search of food. When the drought ended and food was again available, the jack rabbits dispersed throughout their normal range. Field observations indicated that north of the Arkansas River valley jack rabbits concentrated because of a lack of suitable daytime resting habitat.

Recorded jack rabbit population fluctuations in Kansas are apparently as much a function of these concentration and dispersion movements as they are of actual increases or decreases in population size. It is theorized that early in the 1952-'56 period, drought and overgrazing were factors which increased the carrying capacity of certain areas for jack rabbits and the population increased. As the drought intensified the denuded areas could no longer support the larger population and the animals concentrated because of a lack of food and/or daytime resting areas.

It is suggested that concentration and dispersion movements similar to those found in this study could be interpreted as actual changes in over-all population size in other situations, particularly where only censusing data from limited localities are available.

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THE EFFECT OF NATURAL WINTER TEMPERATURES ON DEVELOPMENT OF *ANOPHELES QUADRIMACULATUS* IN SOUTHWESTERN GEORGIA

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Introduction

The development of a colonized strain of *Anopheles quadrimaculatus* Say ova and larvae at natural winter temperatures in southwestern Georgia was studied from December 1, 1951, through June 30, 1952.

Previous studies in this area indicated that fluctuations in populations of adult *A. quadrimaculatus* between April and November were associated closely with temperatures at the water surface in the larval environment (Goodwin and Love 1957). The experiment reported here was undertaken to extend information concerning the relation of naturally occurring temperatures to larval development in nature. Specifically, the study was designed to determine the winter tem-

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peratures in nature which were lethal to *A. quadrimaculatus* ova or larvae and the extent to which larvae would develop under natural conditions.

Few studies have been made previously on development of *A. quadrimaculatus* at low temperature. Huffaker (1944) compared the development time for *A. quadrimaculatus* larvae exposed to constant and fluctuating temperatures and at natural temperatures during the normal breeding season. The effects of cold on other mosquito species have been studied by Davis (1932) for *Aedes aegypti* and Farid (1949) for *Culex pipiens* and *C. quinquefasciatus*. A more recent study of the effect of temperature on mosquitoes was that of Barr (1952), who compared the effect of exposure to a constant temperature of 42° C on all immature stages of *A. quadrimaculatus, A. aztecus* (Hoffman), and *A. freeborni* (Aitken). (Barr's work also includes a summary of studies on the relation of temperature to development.)

From studies on the emergence of *Aedes* in Canada, Haufe and Burgess (1956) devised mathematical expressions of relation between some climatic conditions—temperature, dry cooling power of the atmosphere, daily amount of sunshine—and the daily average of temperature in breeding places. Useful techniques were described for correlating climatic factors and for predicting time of emergence of adult mosquitoes from field data. Although this paper is not concerned with *Anopheles,* it should be consulted for methods and discussion of effects of temperature on development.

Material and Methods

Each day from December 1, 1951, until June 6, 1952, with five exceptions, ova deposited the previous night were removed from the colony cage in the insectary colony room (temperature 78° F) and 25 were transferred to each of 4 biological specimen bowls of 350 ml capacity. The bowls contained untreated well water to a depth of approximately three-quarters of an inch and were provided with wax paper rings which kept ova from adhering to the sides of the bowls. Immediately after preparation the bowls were placed on an open porch of the insectary. Each bowl of ova was checked daily for hatching and larval development. To insure accuracy all larvae were removed with a pipette to depression plates before counting. The containers then were rinsed and refilled with fresh water of the same temperature before larvae were replaced. Once each day powdered dog biscuits were sprinkled on the water in all bowls containing larvae. Pupae were removed from the containers and placed in 1-ounce shell vials plugged with cotton. The analyses reported here are based on 182 series, 728 bowls containing 18,200 ova from which 827 adult mosquitoes were produced.

Continuous records of water temperatures were obtained by a recording thermograph with the sensing element in an enamel pan containing water to a depth of three-fourths of an inch. Temperature summation was used as an expression of time-temperature relationships in the analyses of the data. The basis for selecting this technique is considered in the discussion. The hourly temperature readings for each day were tabulated from the thermograph charts and these values were added to determine the daily number of hour degrees above 0° F.

Results

Figure 1 shows the date on which each batch of ova hatched, the dates on which surviving larvae developed to each succeeding instar, and the mean water temperature. Since plotting of each point in Figure 1A would overcrowd the illustration, only points at which the trend was reversed were indicated. Figure 1A shows in a vertical plane the number of days which elapsed between oviposition and each succeeding larval instar. Where no succeeding stages were indicated, none of the specimens survived. The points were connected to enable easy comparison of intervals between the different instars. No implication of continuity of data on the horizontal (date) scale is intended. The number of days from oviposition to development of successive stages may be determined from Figure 1 as follows: (1) Visualize a vertical projection of the date line in Figure 1B. (2) Note the point where this projected line intercepts the horizontal lines of Figure 1A which depict trends in time of development of the various instars. (3) Determine the number of days from the scale on the abscissa.

The diagonal lines in Figure 1A were extended from the date lines, and indicate the approximate dates on which development had progressed to the stage indicated. The date lines were slanted to emphasize the wide variations in development of successive lots of larvae exposed to essentially the same mean temperature. Note, for example, that the date line for April 20 crosses the third instar line 5 times. This indicates that on April 20 the largest number of second instar larvae from each of 5 lots of ova obtained on 5 different dates reached the third instar on the same day. The slope of the date lines in Figure 1A is such that the interval of time reflected on the abscissa scale is the same as the interval indicated from the origin

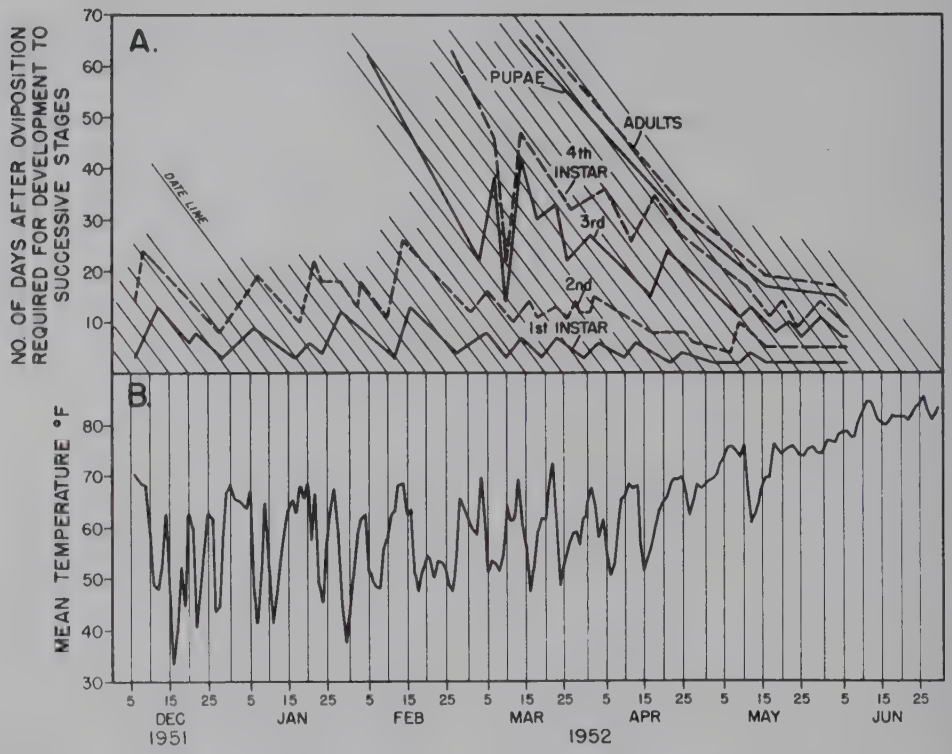

FIG. 1. A. Number of days between oviposition and each successive developmental stage of *A. quadrimaculatus* observed from December 1951 to June 1952. B. Mean water temperature in the experimental containers.

of the ordinate line to the vertical date line of Figure 1B. Vertical date lines were omitted from Figure 1A to reduce crowding. The mean water temperatures for the dates are shown in Figure 1B. The total number of each larval stage extant in the entire series on any date is shown in Figures 2 and 3.

During December, January, and February, when the lowest temperatures occurred, first instar larvae developed slowly to the second stage. Development was accelerated, and the number of second instar larvae increased rapidly when the daily mean temperature was above 60° F. During subsequent cold periods when the daily mean temperature dropped to approximately 45° F approximately 90% of both first and second instar larvae were killed in about equal proportions. This pattern continued until March 10 after which date temperatures were not low enough to cause significant mortality. Subsequently, second instar larvae developed slowly to succeeding stages. The first pupae were obtained May 14, and the first adult May 18; both specimens were from ova of the March 28 series. March 26 was the earliest date from which larvae completed development and adults emerged; the first adult was obtained from this series on May 24.

A method was devised for determining the temperature below which no embryonic development occurred from the records of temperature between oviposition and hatching of the first larva in each lot of ova. The total number of hour-degrees above 0° F from time of oviposition to hatching of the first larva was computed for each series of ova (broken line of Figure 4A). These figures were listed in order of magnitude disregarding the dates of oviposition and hatching. In graphic form, a marked grouping in series separated by distinct gaps is revealed. This is shown by the solid line of Figure 4A, which has no reference to the dates on the ordinate scale. Each group represented series which hatched in the same number of days after oviposition; *e.g.*, all series of ova which hatched in 3 days had required from 4,400 to 5,000 hour-degrees above 0° F; 4 days, 5,600 to 6,300; 5 days, 6,600 to 7,400; 6 days, 7,800 to 8,500. An average was calculated for each group to obtain a mean figure for the num-

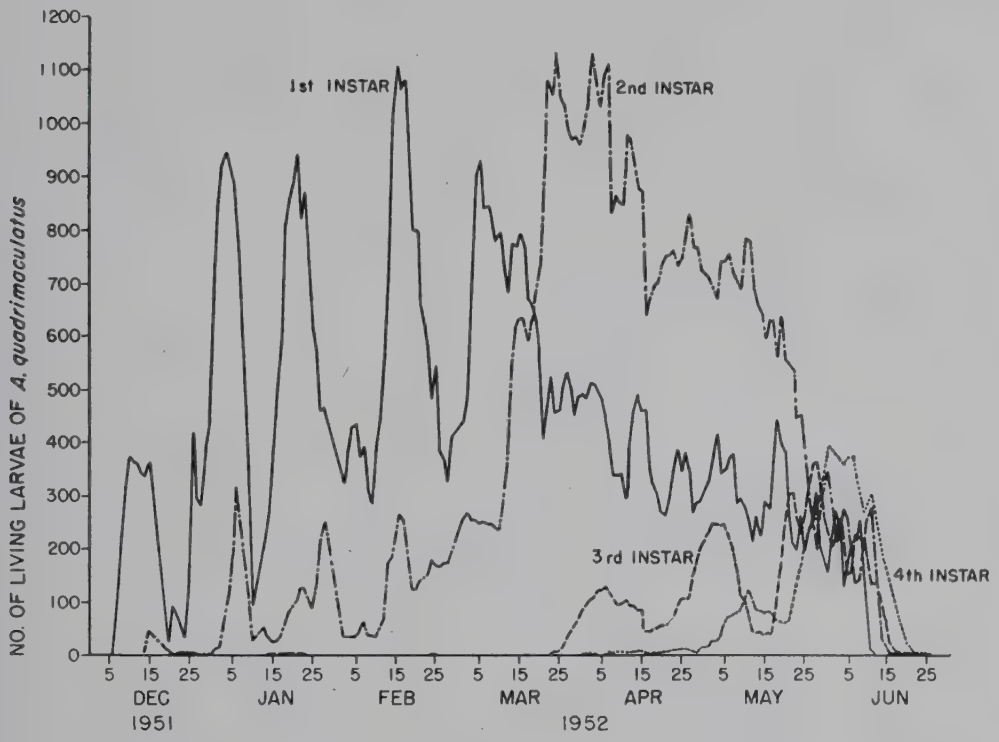

FIG. 2. Total number of each instar of *A. quadrimaculatus* larvae extant on each day from December 1951 to June 1952.

ber of hour-degrees accumulated by ova which hatched on successive numbers of days after oviposition.

To illustrate, ova which hatched in 3 days were exposed to an average of 4,700 hour-degrees. This figure includes for the 3-day period the time expressed as hour-degrees during which the embryos were developing plus the time spent below the point of developmental zero. The average figure of 5,900 hour-degrees for ova which hatched in 4 days includes the time or hour-degrees above developmental zero required for embryonic development plus the number of hour-degrees below the developmental zero during the 4-day period. The difference, 5,900 minus 4,700, probably indicates the additional hour-degrees below developmental zero accumulated during the extra 24 hours of exposure. This figure divided by 24, to reduce hour-degrees to degrees, is the approximate temperature at which no embryonic development occurs. In this study the differences between the average number of hour-degrees on successive days was approximately 1,130. This figure divided by 24 indicates that approximately 47° F is the point of developmental zero.

The number of hour-degrees above 0° F less

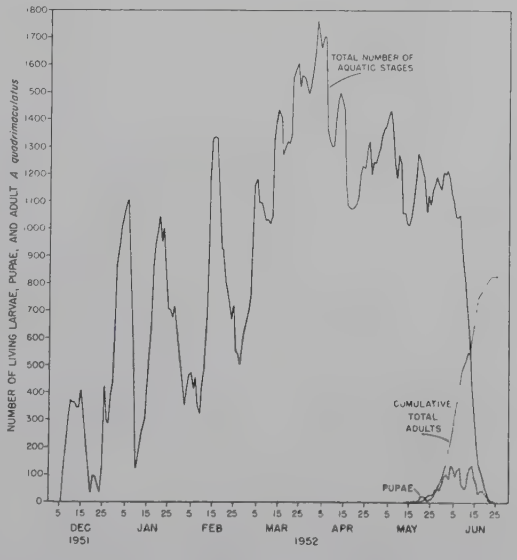

FIG. 3. Total number of larvae, pupae and adult *A. quadrimaculatus* extant on each day from December 1951 to June 1952.

the total obtained by multiplying 47 × 24 × the number of days between oviposition and hatching

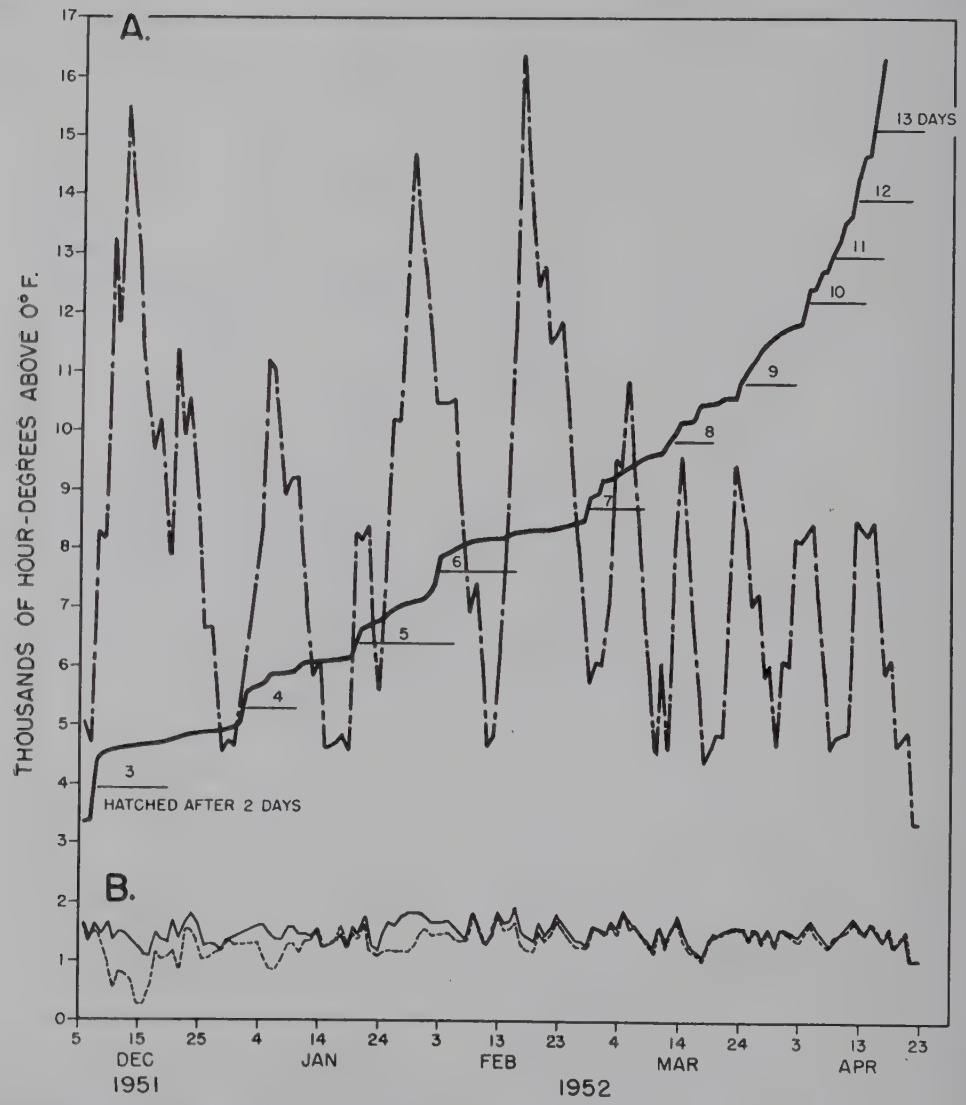

FIG. 4. A. Broken line shows number of hour-degrees above 0°F between oviposition and hatching of *A. quadrimaculatus* shown by dates of oviposition. Solid line shows number of hour-degrees above 0°F between oviposition and hatching arranged in order of magnitude without reference to date of oviposition. B. Interval between oviposition and hatching of *A. quadrimaculatus* shown as number of hour-degrees minus 47 x 24 x the number of days required for hatching (broken line) and corrected for time of exposure to temperatures below 47°F (solid line).

when corrected for the time of exposure to temperatures below 47° F gave a figure of approximately 1,478, range 400 hour-degrees, above 47° F necessary for hatching. This is shown graphically in Figure 4B. The broken line of this figure shows the number of hour-degrees between oviposition and hatching minus 47 × 24 × the number of days required for hatching. The solid line indicates the correction for time of exposure to temperatures below 47° F. This correction was necessary to prevent excessive substractions for periods when temperature remained below 47° F. The indicated time required for embryonic development at 83.5° F (28.6° C) was calculated

to enable comparison with the observations of Huffaker (1944) and Hurlbut (1943). According to this study the period is 40.5 hours, which is close to 39 and 37.7 hours determined by Huffaker and Hurlbut respectively.

The percentage of ova which hatched in each series varied from 25 to 87. Temperature to which ova were exposed seems to have had no effect on the proportion which hatched. Larvae were obtained from 68.2% of all ova which hatched within 2 days; 66.9% from those which hatched in 5 days; 63.3% in 9 days; and 67.5% in 13 days. Larvae were produced by 65.1% of the 18,200 ova used in this study. By month of oviposition, the proportion of ova which produced larvae was: 69% in December, January, February, and May; 64% in March; and 55% in April. Attempts to correlate these differences with the temperatures of March and April failed to show conclusive results.

First instar larvae hatched from each series of ova used in the study. At one time in December all water in containers was frozen for a period of 2 days, but some ova from each series present hatched when the weather became warm. Using approximately the same method described for computing the developmental zero point for ova, the number of hour-degrees required for development of the first instar larvae was calculated. In this case, however, the minimum point is not developmental zero but is the lowest temperature or number of hour-degrees at which most larvae will develop to the next stage. Time of development from first to second instar larvae showed considerably more variation among individuals in a series than did the hatching of ova. The figures used in this calculation were taken from the days on which the greatest number of larvae developed to the succeeding stage. This procedure, of course, eliminated the specimens which developed rapidly or slowly, but the residual specimens should provide data on mean time of development. By this method, the lowest temperature at which most larvae would develop to the second instar was calculated as 57° F. From the temperature data it was determined that 1,000 to 1,500 hour-degrees above this point were necessary for development to the second instar. The developmental time from hatching to second instar larvae ranged from 3 to 23 days.

With only 2 exceptions, second stage larvae were obtained from each series studied. Using the same method, 60° F was calculated as the lowest temperature at which most second instar larvae developed to the third instar. It could not be determined from the data available whether development of second instar larvae halted completely at temperatures below 60° F or if development proceeded at a greatly reduced rate. The times between appearance of the first second instar larvae and the first third instar larvae ranged from 1 to 40 days among the various series.

Although a few third instar larvae were obtained during January and February, none survived more than a few days (Figure 1). Third instar larvae were present continuously after March 23. Computations used for earlier instars indicated that third instar larvae would continue development at any temperature which permitted development from the second stage. Third instar larvae were produced by nearly every series of ova following February 22. Fourth instar larvae were obtained from the series of March 26 and each one thereafter. The time of development for all stages became progressively shorter as the mean temperature rose. The first adult, obtained May 18, required 51 days to develop. Ova of June 6 produced adults in 15 days.

Discussion

This study was designed to provide indications of developmental patterns and rates of survival of ova and larvae under natural winter temperatures when antecedent conditions had been satisfactory for ovarian development. Frequent warm periods are characteristic of the winter season in the latitude of the study area and oviposition probably occurs when temperatures are favorable. Previous studies in southwestern Georgia have shown that ovarian development in some *A. quadrimaculatus* proceeds during the winter months (Zukel 1949a). Larvae in nature, however, are very scarce or absent during the coldest periods of the winter. Intensive searches failed to disclose specimens in January and February (Zukel 1949b).

This experiment was not designed to duplicate conditions in nature. Attempts were not made, accordingly, to place ova under ambient conditions immediately after oviposition. Most of the ova were probably 12 to 14 hours old at the time of transfer to the outdoor insectary, and hence development of the embryo to the first instar could have been about one fourth completed. The validity of the mathematical computations used to determine points of base line development for ova probably was not affected significantly by the initial exposure to higher temperatures, since ova were transferred to the open insectary at approximately the same time each day. In effect, the analysis is on a consistent fraction of the em-

bryonic development. Hence, the computed number of hour-degrees required for hatching may be slightly in error. Considering, however, that the methods used in this study were not conducive to accuracy within 2 or 3 degrees, the figure of 47° F calculated for developmental zero is in close agreement with Huffaker's (1944) computation of developmental zero at 7° C (44.6° F).

Occurrence of temperatures below 47° F may also affect the accuracy of these calculations. The degree of error in both cases is small as attested by the distinct grouping in the magnitudinal listing of hour-degrees and the close agreement with duration of developmental periods calculated in other studies. The greatest effect of the low temperature would be an increase in the spread within a group and the largest errors would occur in series which required the greatest number of days for development. Time of development between oviposition and hatching of given series ranged from 2 to 13 days.

This experiment was undertaken as a collateral laboratory study to aid in the interpretations of field observations. The results are not indicative of critical relationships between temperature and the rate of development. Mathematical treatments were selected carefully to avoid implication of more precision than warranted by the data available.

It should be kept in mind that these experiments were conducted with material from an established laboratory colony. Interpretations of results with respect to behavior of sylvan *A. quadrimaculatus* should be made with this reservation.

Huffaker (1944) in reviewing some of the attempts to devise suitable formulae for expressing mathematically the relation between developmental time of mosquito larvae and temperature emphasized objections to the technique of thermal summation. Use of hour degrees derived by summation of the daily increments has serious limitations for physiologic studies. The use of the technique in this paper does not imply proposal of a linear relationship between temperature and time of development. No satisfactory methods have been devised for determining the nature of this relationship for mosquito larvae reared under variable temperatures. Hurlbut (1943) has shown, however, that temperature summation is a practical method for predicating growth rates of the aquatic stages of *A. quadrimaculatus* under natural conditions. This assumption was based on studies of development at constant temperatures and at variable temperatures in the field.

Under conditions of these observations, the first adults of the spring were obtained May 18 from ova of the March 28 series. In this area, adult *A. quadrimaculatus* usually appear considerably earlier (Goodwin and Love 1957). In Zukel's (1949b) studies adult males were collected in these same areas on March 7. By projecting backward from this date the appropriate number of hour degrees required for development of the aquatic stages, he calculated that ova must have been deposited in late January or early February. Air temperature differences at the time of the present study were compared with Zukel's study do not account for differences in time of spring emergence. The severity of conditions in the experimental study was more likely responsible. Changes in water temperature were more abrupt and extreme in the limited environment of the dishes than in natural ponds. In 1952 the first field collected *A. quadrimaculatus* adult was taken on March 27.

Data from the present study are compatible with observations of Hurlbut (1943) and Huffaker (1944) which indicate that larvae of *A. quadrimaculatus* did not survive when average daily water temperatures were below 50° F. Comparison of Figures 1B and 3 shows definite drops in the number of surviving larvae when temperatures fell below 50° F. Not until after February were temperatures consistently high enough to sustain a progressive increase in the number of aquatic stages. The effect of low temperatures after February are clearly reflected by data in Figure 3.

Larvae hatched from each series of ova observed in this study. This may be attributable to the impetus to development before ova were moved to ambient conditions. The fact that second stage larvae also developed from all except 2 series suggests the possibility that the early instars are more resistant to low temperatures. Huffaker (1944) found that the optimum temperature for development was highest for ova and progressively lower for each larval instar. However, regular intensive searches of prolific breeding places over a period of 12 years have failed to indicate different patterns of survival for the various larval instars in nature.

The calculations of developmental thresholds in this study follow generally the form ordinarily used in controlled laboratory experiments such as those cited above. The objective of the present investigation, however, was to develop an approximation of the ecological temperature zero. As defined by Allee *et al.* (1949), in the lower temperature range the highest externally imposed temperature at which development cannot be successfully completed is the ecological temperature

zero. Because of inherent variability of the organisms, the difficulty of relating relatively coarse measurements to specific microenvironment, and the lack of uniformity in handling and feeding specimens, a precise expression could not be expected. The data obtained generally corroborate related experimental studies and provide information for substantiation of field observations.

In a previous report, the pronounced detrimental effect of high temperatures on populations of adult *A. quadrimaculatus* was indicated (Goodwin and Love 1957). The present study shows similar detrimental effect of low temperature on larval stages. Predictions of development cannot be predicated on the heat budget (hour-degrees) or mean temperatures alone but must consider also the extreme condition even though they may be infrequent and transitory.

In the area studied, adult *A. quadrimaculatus* did not develop until mean daily temperature remained consistently above 60° F, and significant increments to the population did not occur until mean daily temperatures were sustained above 70° F. The impression was obtained that development was more rapid when daily maximum temperatures remained in the higher portion of the optimum range and that speed of development was not related directly to the heat budget, *i.e.* the relation between rate of development and temperature is not linear. After development had been suppressed by low temperatures, many series of larvae from ova obtained over a period of several days would reach the next stage simultaneously. This resulted in very abrupt increases in larval and adult populations. Explosive appearance of adult *A. quadrimaculatus* in the spring probably is due to such a pattern of development and, in this latitude, not to the emergence of hibernating adult mosquitoes. The occurrence of a normal proportion of male mosquitoes in the first spring brood also indicates that the initial population was not in hibernation. Similarly, some variations in population during the breeding season probably result from the variations in rates of development and not from emergence of discrete generations as has been suggested.

Summary

Observations were made on development of ova and larvae from a colonized strain of *A. quadrimaculatus* at natural winter temperatures in southwestern Georgia. No ova hatched at temperatures below 50° F; 90% of first and second instar larvae were killed by temperatures of 45° F. The point of developmental zero for ova was calculated as approximately 47° F. Approximately 1,500 hour-degrees above 47° F were necessary for hatching. Mean temperature of approximately 57° F was computed as the lowest temperature at which most first instar larvae would develop to the second instar. Mean temperature above 60° F was necessary for most second instar larvae to develop to the third instar. Under natural temperatures, the developmental time from ova to adult varied from 15 to 51 days.

Adult *A. quadrimaculatus* were not produced until mean daily temperatures remained consistently above 60° F. When a mean temperature of 70° F was reached, development of larvae which had been retarded by low temperature advanced rapidly and adult mosquitoes from ova produced over a period of several days emerged simultaneously. This probably accounts for the explosive appearance of *A. quadrimaculatus* in the spring.

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PARASITES OF SINGAPORE MOSQUITOES, WITH PARTICULAR REFERENCE TO THE SIGNIFICANCE OF LARVAL EPIBIONTS AS AN INDEX OF HABITAT POLLUTION[1]

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INTRODUCTION

Much of the extensive but scattered literature on the parasites of mosquitoes is summed up in the papers of Speer (1927) and Christophers (1952). Many of the published records are adventitious ones resulting from chance observations during larval surveys and other investigations not primarily parasitological in nature. Some mosquito parasites such as fungi of the genus *Coelomomyces* and microsporidan protozoans are highly pathogenic. Others are less so, and undue emphasis has sometimes been placed on associations between mosquitoes and microorganisms, particularly larval epibionts such as vorticellid ciliates, without reference to broader aspects of habitat ecology.

An 18-month insect quarantine project at Singapore Airport (Laird 1956b) presented an opportunity to make a detailed study of the ecology of a wide range of mosquito larval habitats. It is the purpose of this paper to consider the significance of the parasites recorded in the investigation, together with that of pathogens from adult mosquitoes collected elsewhere on Singapore Island.

The term "parasite" as used herein is meant to be understood in its widest sense, covering epibionts and endobionts of every kind without reference to the nature of host relationships.

METHODS

Monthly samples of mosquito larvae and any other animals, plants and detritus present in the stations under investigation, were brought to the laboratory for study in the living state. Fresh material was examined by phase-contrast, dark field and bright field techniques. Permanent preparations were fixed in Worcester's fluid and stained with Delafield's or Heidenhain's haematoxylin, or—especially in the case of bacteria—nigrosin or Giemsa.

All figures were prepared with the aid of a Zeiss-Winkel drawing apparatus, and all averages are derived from the measurements of 50 successive examples.

Larval epibionts were seldom recorded from container-breeding mosquitoes, most of those discovered occurring in freshwater ponds, ponded streams and transient pools. The temperature and hydrogen ion content of the water in these habitats, all of which were on laterite, proved relatively constant. Daytime water temperatures were usually within the limits of 26° C and 32° C, the pH (estimated by means of a Lovibond comparator) ranging from 6.4 to 7.0. The stations were all exposed to sunlight in flat, open country. Pollution was a major factor determining the composition of their flora and fauna.

Some understanding of the biological consequences of water pollution is necessary for proper appreciation of the nature and significance of mosquito larval epibionts.

THE ESTIMATION OF WATER POLLUTION BY BIOLOGICAL METHODS

The classification of the degrees of water pollution followed herein is that of Kolkwitz and Marsson (Kolkwitz 1935, Liebmann 1951). All data in this section are drawn from the present field studies. Most of the animals and plants concerned proved referable to widely distributed species, although many of them had not been recorded from Singapore before. From the number of specific names appearing in bold face to indicate their having been listed under the appropriate headings by Kolkwitz and Liebmann, it will be seen that this system, although designed under temperate European conditions, is equally applicable in the tropics. Information on most of the species mentioned is available in the works already named and in Bergey (1934—Bacteria), Prescott (1951—Algae) and Kudo (1954—Protozoa).

Neither katharobic conditions (those of highest purity, as found, for example, in mountain freshets) nor oligosaprobic ones (those under which the oxidation of polluting substances is almost complete) were met with in this project. My larval epibionts all originated from mesosaprobic or polysaprobic waters, and it is proposed to deal with these alone.

[1] Contribution from the Institute of Parasitology, McGill University, Macdonald College P.O., Que., Canada. All material was collected while the author was on the staff of the Department of Parasitology, University of Malaya, Singapore, to which thanks are expressed. Abstract read at the Tenth International Congress of Entomology, Montreal, August 17-25, 1956.

Polysaprobic conditions are characterized by heavy pollution and decomposition, with reduction of the polluting substances proceeding vigorously. Mesosaprobic conditions prevail through most of the zone of oxidation; amino acids characterize the *a*–mesosaprobic subdivision, and under β–mesosaprobic conditions further oxidation takes place and the ammonia compounds of the fatty acids are evident. The occurrence and relative abundance of a variety of organisms, particularly certain cosmopolitan bacteria, algae and protozoans, serve to indicate which of these 3 sets of conditions prevails.

β–mesosaprobic waters support a rich and diverse fauna and flora in which most of the groups of clean-water animals and plants are represented. The Singapore Airport area includes great numbers of ponds, notably fish ponds and "hyacinth ponds"—maintained by Chinese smallholders for the cultivation of water hyacinth, *Eichhornia crassipes* (Mart.), for pig fodder—that often fulfil the necessary conditions. Marsh pools and other natural surface waters not too heavily contaminated by grazing animals also belong here, as do various container habitats. β–mesosaprobic surface waters support a wide range of emergent plants, such floating but rooted perennials as *Eichhornia* and **Nymphaea,** and free-floating species including *Pistia stratiotes* L. and duckweeds of the genera **Lemna**, *Spirodela* and *Wolffia*. Many of the green algae characteristic of oligosaprobic waters flourish here too. Free-living bacteria occur, although seldom in very heavy concentration, but the sessile species **Sphaerotilus dichotomus** (Cohn) and *Siderocapsa Treubii* Molisch may be common on various substrates. Diatoms and desmids may be conspicuous, especially encrusting diatoms such as **Melosira** spp.; and planktonic Chlorococcales including **Pediastrum Boryanum** (Turp.), **Ankistrodesmus** spp., **Scenedesmus** spp. and **Selenastrum** spp. are very evident at times. Epibiotic algae of the genus *Characium* occur on microcrustaceans. A great variety of phytoflagellates (**Euglenidae**) are to be found. Other characteristic free living protozoans include the sarcodinids **Amoeba proteus** (Pallas), **Amoeba radiosa** (Ehrenberg), **Arcella vulgaris** Ehrenberg and *Centropyxis aculeata* Stein, the heliozoans **Actinosphaerium eichhorni** Ehrenberg and **Actinophrys sol** Ehrenberg, and the ciliates **Aspidisca lynceus** Ehrenberg, **Bursaria truncatella** Müller, **Coleps hirtus** (Müller), **Euplotes** spp., **Halteria grandinella** (Müller) and **Loxophyllum** *meleagris* Dujardin. Among the higher groups found here are **Hydra** spp., annelids including **Stylaria** spp., many different rotifers (especially facultative epibionts of the genus **Brachionus**), cyclopids, cladocerans, ostracods, decapods, insects of most of the aquatic families, snails and fishes. An abundance of food, the opportunities for shelter and other relationships provided by a prolific growth of phanerogams and filamentous green algae, and the relatively low concentration of deleterious substances in the water render β–mesosaprobic conditions tolerable to numerous different mosquitoes. The diversity of animal and plant substrates under suitable chemical and physical conditions favours the development of a varied fauna of protozoan epibionts. These include the flagellates *Codosiga utriculus* Stokes, *Phalansterium digitatum* Stein and *Poteriodendron petiolatum* (Stein), spirotrichous ciliates of the genus **Stentor,** peritrichous ciliates of the genera *Campanella, Epistylis, Lagenophrys, Opisthonecta. Platycola, Pyxidium, Scyphidia* and **Vorticella**, and such suctorians as **Acineta** spp.

The flora and fauna of *a*–mesosaprobic waters are much less representative than those just considered. Free living bacteria, notably **Spirochaeta plicatilis** Ehrenberg, are much more abundant, and *Sphaerotilus dichotomus* flourishes once again. Relatively few green algae occur, although individual plankters like **Chlorella** spp. and the desmids *Closterium acerosum* (Schrank) and **Cosmarium Botrytis** Meneghini are sometimes present in very large numbers. The place of filamentous Zygnemataceae is taken by blue-green algae, particularly **Oscillatoria** spp. and **Phormidium** spp. Some phanerogams such as *Eichhornia* and the Lemnaceae are able to exist under *a*–mesosaprobic conditions, but the higher plants are seldom conspicuous. Colourless flagellates assume some prominence, characteristic species being **Astasia klebsi** Lemmermann, **Bodo** *caudatus* (Dujardin), **Chilomonas paramecium** Ehrenberg and **Peranema trichophorum** (Ehrenberg). The phytoflagellates are less well represented, although the genera *Phacus* and *Trachelomonas* may be prominent and **Cryptoglena pigra** Ehrenberg, *Euglena fusca* (Klebs), *E. haematodes* (Ehrenberg), *E. spirogyra* Ehrenberg and *Lepocinclis ovum* (Ehrenberg) are plentiful at times. Prominent free-living ciliates are **Amphileptus clapareidi** Stein, **Chilodonella cucullulus** (Müller), **C. uncinata** (Ehrenberg), **Colpoda cucullus** Müller, **Cyclidium** spp., **Paramecium caudatum** Ehrenberg, **Spirostomum ambiguum** Ehrenberg, **Stylonychia mytilus** (Müller), *Tetrahymena* (= **Glaucoma**),

pyriformis Ehrenberg, **Oxytricha fallax** Stein and **Urocentrum turbo** (Müller). **Tubifex** spp. and other annelids, especially small Naididae, are often abundant. The representation of rotifers is generally reduced, with greater emphasis upon the Bdelloidea, but species of **Brachionus** may be common. The crustacean fauna is chiefly composed of a few individually abundant cyclopids and, to a lesser extent, cladocerans. These are frequently heavily infested with *Characium*, the phytoflagellate *Colacium vesiculosum* Ehrenberg, peritrichous ciliates and suctorians. Gastrotricha are common in detritus, and some snails and fishes still occur. The insect fauna is impoverished, although individual species may be abundant. The best represented insect orders are the Hemiptera, Odonata and Diptera, particularly the last; larvae of several species of Culicidae, Heleidae, Stratiomyiidae and Tendipedidae may flourish. There is a much less varied fauna of epibiotic protozoans than under β–mesosaprobic conditions. Some stalked peritrichous ciliates flourish on various plant and animal substrates, *Epistylis lacustris* Imhoff and **Vorticella convallaria** (L.) being characteristic. *Vorticella microstoma* Ehrenberg is common, and the stalked suctorian **Podophrya** *collini* Root may become prominent.

The aquatic bacterial flora reaches its peak in polysaprobic waters. Characteristic free-living species are **Streptococcus margaritaceus** Schroeter, **Proteus vulgaris** Hauser, **Spirillum undula** (Müller) and *S. volutans* Ehrenberg. Attached forms flourish, notably **Beggiatoa alba** (Vaucher), **Sphaerotilus natans** Kützing and **Zoogloea ramigera** Itzigsohn, and *S. dichotomus* persists into the zone. A few diatoms may be present, but the algal flora is overwhelmingly dominated by the blue-green genera **Oscillatoria** and **Spirulina.** The chief free living protozoans are colourless flagellates, notably **Bodo** *caudatus* (Dujardin), *Copromonas subtilis* Dobell, **Hexamita inflata** Dujardin, **Polytoma uvella** Ehrenberg and **Trepomonas rotans** Klebs. **Oikomonas** *termo* (Ehrenberg) is often abundant in the remains of dead aquatic animals (*e.g.* entomostraca) in company with the ciliate **Tetrahymena pyriformis.** Two species of amoebae, **Pelomyxa palustris** Greeff and **Vahlkampfia limax** (Dujardin), occur commonly, as do the free living ciliates **Caenomorpha medusula** Perty, **Colpidium colpoda** Ehrenberg, **Discomorpha pectinata** L., **Paramecium putrinum** Claparède and Lachmann, **Saprodinium** *putrinum* Lackey, **Tillina magna** Gruber and **Uronema marinum** Dujardin. Free-living suctorians of the genus **Sphaerophrya** are sometimes present in large numbers, and have been observed feeding upon **Spirillum. Tubifex** abounds under polysaprobic conditions, and the characteristic rotifers are bdelloids. Cyclopids are the chief representatives of the Crustacea. Few insects other than Diptera occur, and still fewer are well adapted to polysaprobic conditions. Those that are, though, belong to a wide range of families, the Culicidae, Drosophilidae, Heleidae, Psychodidae, Syrphidae and Tendipedidae all being represented in such habitats at Singapore. The epibiotic fauna and flora are limited, but highly characteristic. **Vorticella microstoma,** the dominant protozoan, is often present on various substrates in association with **Sphaerotilus** and **Zoogloea.** The colourless flagellates *Pleuromonas jaculans* Perty and *Monas* sp., both of which occur in the plankton as well, often temporarily anchor themselves by the tip of a flagellum. *Podophrya collini* sometimes persists from the α–mesosaprobic zone.

A few of the ponds studied at Singapore Airport—notably small, permanent ones in pig pens are constantly polysaprobic. Large fish ponds and hyacinth ponds close to habitation and subject to continual manuring from a sty located at one of the edges or a latrine built out over the water, have fairly well defined polysaprobic, α–mesosaprobic and β–mesosaprobic zones. The whole sequence from one extreme of pollution to the other may be followed by regular observations at small hyacinth ponds some distance from houses and sties, and consequently only sporadically manured. Similar sequences may be traced in natural water bodies such as transient pools and marsh ponds exposed to grazing animals and subject to radical alterations in volume through rainfall, evaporation and changes in the level of the water table. In all cases, flooding following heavy rain brings about a temporary lowering of the pollution level.

Most of the container habitats dealt with, concrete troughs, metal drums and tanks, discarded tires, cans and the like, yield a mesosaprobic microflora and microfauna. Highly polysaprobic conditions are of course the rule in latex cups, earthenware jars used for the storage of liquid manure, and rat-gnawed coconuts containing a thick fluid heavily charged with decomposing copra. However, the variety of microorganisms present is always limited by comparison with surface waters. Epibionts are rare, particularly in such artificial containers as drums, tires and cans.

Mosquito Larvae and Pollution

Larvae of 22 species of mosquitoes were collected in the vicinity of Singapore Airport and examined for parasites. The number in brackets after each name in the following list indicates the number of positive stations (out of a total of 164 studied).—

1. *Anopheles* (*Anopheles*) *hyrcanus* Pallas (Probably more than one subspecies was involved, but as identifications were based on larval characters alone this insect is referred to hereunder simply as *An. hyrcanus*). (*23*)
2. *An.* (*Myzomyia*) *kochi* Dönitz. (*55*)
3. *An.* (*Myzomyia*) *sundaicus* Rodenwaldt. (*1*)
4. *Uranotaenia atra* Theobald. (*1*)
5. *U. nivipleura* Leicester. (*2*)
6. *Ficalbia* (*Mimomyia*) *metallica* Theobald. (*6*)
7. *Taeniorhynchus* (*Mansonioides*) *uniformis* Theobald. (*3*)
8. *Aëdes* (*Stegomyia*) *aegypti* L. (*1*)
9. *A.* (*Stegomyia*) *albopictus* Skuse. (*39*)
10. *A.* (*Rhinoskusea*) *longirostris* (Leicester). (*1*)
11. *Armigeres* (*Armigeres*) *obturbans* Walker. (*9*)
12. *Culex* (*Lutzia*) *fuscanus* Wiedemann. (*17*)
13. *C.* (*Culex*) *annulus* Theobald. (*15*)
14. *C.* (*C.*) *bitaeniorhynchus* Giles. (*15*)
15. *C.* (*C.*) *fuscocephalus* Theobald. (*22*)
16. *C.* (*C.*) *gelidus* Theobald. (*16*)
17. *C.* (*C.*) *mimulus* Edwards. (*1*)
18. *C.* (*C.*) *nigropunctatus* Edwards. (*3*)
19. *C.* (*C.*) *pipiens fatigans* Wiedemann. (*18*)
20. *C.* (*C.*) *pseudovishnui* Colless. (*8*)
21. *C.* (*C.*) *sitiens* Wiedemann. (*1*)
22. *C.* (*C.*) *tritaeniorhynchus siamensis* Barraud and Christophers.* (*51*)

An. sundaicus, A. aegypti, C. mimulus and *C. sitiens* were not represented in the Airport collections at the time of preparation of the account of quarantine aspects of this project (Laird 1956b), in which details of the utilization of various types of larval habitats by the other species are to be found.

Only two mosquitoes, *An. sundaicus* and *C. sitiens*, were found breeding in brackish water (at the edge of a mangrove swamp). A third typically brackish water species, *A. longirostris*, was found once only, the record being an adventitious one from a freshwater pond. The developmental stages of the remaining 19 mosquitoes are found in fresh water. *C. p. fatigans, A. albopictus, A. aegypti, U. nivipleura* and *Ar. obturbans* are container breeders, although the first species is often present in surface waters as well. The others are primarily surface water breeders, but some of them—*C. fuscanus, C. fuscocephalus* and *C. t. siamensis* for example—are also recorded from the larger types of simple container from time to time.

Nineteen species figured in collections from β–mesosaprobic waters, the exceptions being *Ar. obturbans, C. gelidus* and *C. p. fatigans*. Certain species found here (*C. bitaeniorhynchus, C. mimulus, C. nigropunctatus* and *C. pseudovishnui*) find their optimum conditions in the better oxygenated waters of oligosaprobic ponds. *An. hyrcanus, F. metallica* and *T. uniformis* reach their peak under β–mesosaprobic conditions, the first-named species in fairly deep water with abundant emergent plants such as water hyacinth, the second in association with Lemnaceae and *Pistia*, and the third anchored to the roots of water hyacinth from which both larvae and pupae derive their air supply. All 3 species tolerate higher than normal levels of pollution in manured fish ponds and hyacinth ponds, provided that these levels are not maintained long enough to adversely affect their plant associates. *An. kochi, C. annulus, C. fuscanus, C. fuscocephalus, C. gelidus* and *C. t. siamensis* all flourish in α–mesosaprobic waters. *C. p. fatigans* is common under such conditions in both ground pools and containers, and the container breeders *A. albopictus* and *U. nivipleura* develop equally well throughout both mesosaprobic zones. The 7 species dominant in α–mesosaprobic surface waters tolerate polysaprobic conditions as well, *C. p. fatigans* reaching its peak in waters highly contaminated by fecal material. The latter species and the container-breeding *Ar. obturbans* are the characteristic mosquitoes of polysaprobic habitats at Singapore.

Larval Epibionts

I. *TAXONOMIC*

Little more than appropriate references are given for species which are well known, or which have recently been described in detail elsewhere. The scheme of classification follows Bergey (1934) for Bacteria, Brumpt (1949) for Fungi, Prescott (1951) for Algae and Kudo (1954) for Protozoa. The number in parentheses after each name indicates the number of positive stations.

* Since the manuscript was written, Colless (1957, Ann. Trop. Med. Parasitol., 51, 87-101) has shown that this name, used by numerous authors for the Malayan subspecies of *C. tritaeniorhynchus*, is a synonym of *C. t. summorosus* Dyar.

BACTERIA

Schizomycetes/Eubacteriales/Coccaceae

Siderocapsa Treubii Molisch (Pl. I, Figs. 1 and 2) (*2*)

Mosquitoes infested.—*An. kochi, C. fuscocephalus, C. gelidus, C. t. siamensis.*

Other substrates.—*Pistia* leaves, surface scum.

Iron deposits on infested larvae appear as brown specks to the naked eye. These deposits surround variously shaped mucoid masses in which are embedded from one to 30 coccoid or bacilloid cells invisible by direct illumination but seen clearly by phase-contrast. The rusty masses about small, circular colonies (Figure 2) range from 3-15μ in outside diameter. Several colonies may become fused into a single sheet (Figure 1) up to 125μ long. Elongate cells measuring 0.6-1.7μ × 0.3-0.5μ are more numerous than coccoid ones (0.4-0.8μ), and are often associated in pairs. Molisch (1909) proposed the name of *Siderocapsa Treubii* for an Indonesian species forming colonies of from one to eight coccoid cells on underwater leaves. He subsequently (1910) described a second species, *S. major,* characterized by colonies of up to 100 or more somewhat elongate cells (0.7-1.8μ) in the scum on stagnant pools. Hardman and Henrici (1939) studied *Siderocapsa* obtained from slides suspended in American lakes and streams. Although some of their colonies corresponded with *S. Treubii* and others with *S. major,* a complete series of intergrading forms could be traced. Considering it impossible to substantiate two species, they referred all their material to *S. Treubii. Treubii* and *major* forms and intermediates were present on mosquito larvae and other substrates at Singapore. All forms are not only morphologically comparable with *S. Treubii* as defined by Molisch (1909) and Hardman and Henrici (1939), but their habitats correspond (The two stations concerned were of pH 7.2 and 8.2, an exceptional state of affairs at Paya Lebar where surface waters are usually acid, and Hardman and Henrici, who only recorded the species from alkaline habitats, stated that "Of the various environmental factors considered, the pH of the water appears to be the most important"), and the rapid rate of development—underlined by the occurrence of well developed colonies on the integument of larvae undergoing frequent ecdyses—is just as described by the American authors, who obtained abundant specimens on immersed slides within a few days.

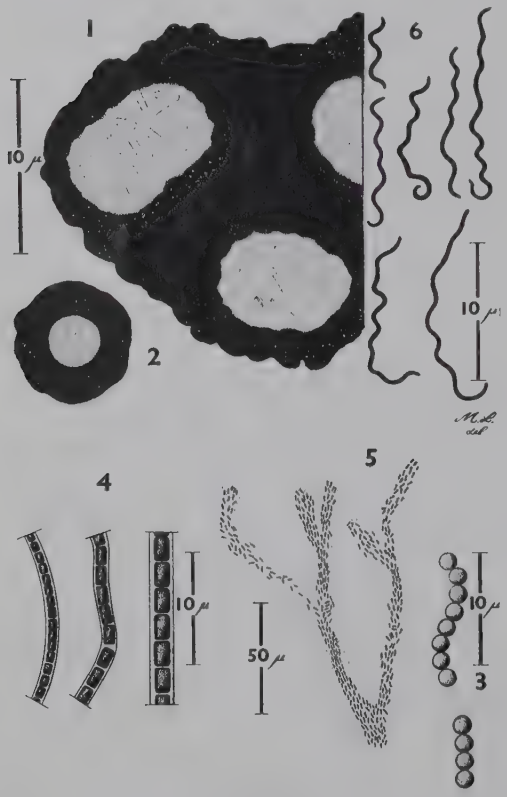

PLATE I

FIGS. 1 and 2. *Siderocapsa Treubii,* from larval *Culex gelidus.* Fresh material, phase-contrast. 4,440x.

FIG. 3. *Streptococcus margaritaceus,* from larval *Culex gelidus.* Fresh material, phase-contrast. 2,850x.

FIG. 4. *Sphaerotilus natans,* from larval *Anopheles kochi.* Fresh material, phase-contrast. 2,850x.

FIG. 5. *Zoogloea ramigera,* from larval *Anopheles kochi.* Fresh material, phase-contrast. 570x.

FIG. 6. *Borrelia culicis,* from larval *Culex mimulus.* Giemsa. 3,500x.

Streptococcus margaritaceus Schroeter (Pl. I, Fig. 3) (*2*)

Mosquitoes infested.—*An. hyrcanus, C. gelidus, C. t. siamensis.*

Occurrence elsewhere.—Free living in the stations concerned.

This gram positive organism forms chains of spherical cells about 1.5μ in diameter, ranging up to 30μ in length (Liebmann, 1951). The chains measured at Singapore averaged 9.0μ in length, with a maximum of 24.0μ and were made up of from four to 12 cells of a diameter of 1.3-1.5μ. Numerous motionless chains adhered to all the body surfaces of the larvae concerned.

Schizomycetes/Chlamydobacteriales/Chlamydobacteriaceae

Sphaerotilus natans Kützing (Pl. I, Fig. 4) (*6*)

Mosquitoes infested.—*An. kochi, C. annulus, C.*

fuscocephalus, C. gelidus, C. p. fatigans, C. t. siamensis.

Other substrates.—Larval Tendipedidae and Anisoptera, submerged pieces of wood, dead vegetation.

Bergey (1934) defined the genus *Sphaerotilus* as "Attached colourless cells showing false branching, making a pseudo-dichotomy. Filaments consist of rod-shaped or oval cells, surrounded by a thin, firm sheath. Multiplication occurs both by non-motile and motile conidia, the latter with a clump of flagella near one end." The genus differs from the closely related *Leptothrix* in that iron is not deposited in the sheath.

S. natans, the genotype, rarely exhibits false branching. Its filaments form macroscopic greyish-white "beards" on objects submerged in polysaprobic waters. Bergey described the cells as cylindrical, the sheath being slimy, difficult to detect, and about 2.0μ thick. Other authors (*e.g.* Liebmann, 1951) have given the maximum diameter of the sheath as 10μ, and the measurements of individual cells as 4-6μ by 2-3μ.

A *Sphaerotilus* from the mosquitoes listed above, was characterized by an unbranched sheath up to 4.0μ thick, individual cells measuring 1.2μ × 0.7μ — 6.0μ × 2.5μ. Both oval and bacilloid cells were seen, the latter being the commonest. The microorganism formed the slimy masses characteristic of *S. natans,* to which it is referred despite the unusually small size of some of its cells.

Sphaerotilus dichotomus (Cohn) (*21*)

Mosquitoes infested.—*An. hyrcanus, An. kochi, A. albopictus, C. annulus, C. bitaeniorhynchus, C. fuscanus, C. fuscocephalus, C. gelidus, C. p. fatigans, C. pseudovishnui, C. t. siamensis.*

Other substrates.—Aquatic plants, submerged objects, Cladocera, Copepoda, Ostracoda, larval Psychodidae, Tendipedidae, Plectoptera, Anisoptera, etc.

Sheathed epiphytic bacteria exhibiting false branching, their bacilloid cells measuring 1.5-4.5μ × 0.8-1.2μ (av., 2.5μ × 1.0μ). This organism is identical with that identified as *Sphaerotilus* aff. *dichotomus* from some South Pacific mosquitoes by Laird (1956a), and it answers to the brief description of *S. dichotomus* published by Bergey (1934). There is some uncertainty as to the correct generic name. Some authorities favour *Cladothrix* Cohn, although Bergey regarded this as a synonym of *Sphaerotilus.*

Zoogloea ramigera Itzigsohn (Pl. I, Fig. 5) (*6*)

Mosquitoes infested and other substrates as for *S. natans.*

Dendriform zoogloeal structures up to 250μ high (usually 100-150μ), each consisting of a freely branching hyaline matrix 6-15μ (av., 10μ) thick, containing great numbers of single or paired ovoid to bacilloid bacteria measuring about 1.0μ × 0.5μ, were present on the thorax and abdomen of many of the larvae infested with *S. natans.* Larger masses (up to 1.25 mm) were abundant on submerged debris. This organism is of identical morphology and habit to that described as *Zoogloea ramigera* Itzigsohn by Huber-Pestalozzi (1938), who remarked upon the frequent association of *Z. ramigera* and *S. natans* on submerged objects in polluted waters in Northern Europe. The Singapore material is referred to *Z. ramigera,* without prejudice to questions of taxonomy raised by those bacteriologists who do not consider *Zoogloea* a valid genus and prefer to regard such forms as multiplicative stages of associated Chlamydobacteriales.

ALGAE

Cyanophyta/Hormogenales/Oscillatoriaceae

Oscillatoria brevis Kützing (*1*)

Mosquito infested.—*A. albopictus.*

Occurrence elsewhere.—In the plankton and at the bottom of the station concerned, a metal boiler.

Ball-like algal masses were formed on the abdomen of infested larvae. Living trichomes exhibited the oscillating and gliding movements characteristic of the genus. Individual cells (as seen in Delafield-stained whole mounts) measure 1.5-3.0μ × 4.1-6.0μ (av., 2.5μ × 5.1μ). The trichomes are straight, except for a terminal curve, and they taper towards the end. There are no constrictions at the cross walls. Ref. Huber-Pestalozzi (1938) and Liebmann (1951).

PROTOZOA

Mastigophora/Euglenoidina/Euglenidae

Colacium vesiculosum Ehrenberg (*1*)

Mosquitoes infested.—*C. annulus, C. fuscocephalus.*

Other hosts.—Cyclopidae.

Stalked individuals from the thorax of culicine larvae measured 10.7-25.5μ × 9.0-14.5μ. They occurred singly and in colonies of two or four, and answered to the description of *C. vesiculosum* as summarized by Prescott (1951) and Kudo (1954). This sessile microcrustacean epibiont was so plentiful on unidentified cyclopids in the station concerned that they appeared green to the unaided eye. The mosquito larval infestations were light, and obviously adventitious.

Phacus curvicauda Swirenko (*1*)

Mosquitoes infested.—*A. albopictus, C. p. fatigans.*

Other substrates.—Larval Psychodidae, moulted exuviae of Belostomatidae.

Singapore examples of this flagellate measure 28.34μ × 21-27μ (av., 31μ × 25μ). Its dimensions were given by Skvortzow (1928) as 24-34μ × 21-25μ, and by Prescott (1951) as (25)-28-30μ × 24-26μ. The flattened, racquet-shaped body contains two paramylon discs and many ovoid chloroplasts. The pellicle is longitudinally striated, and there is a prominent ventral groove. Posteriorly, a sharply pointed caudus curves obliquely to the left (the animal being viewed from the ventral aspect, the side usually uppermost when a mounted cover slip smear is examined microscopically).

Large numbers of flagellates were present along the intersegmental abdominal grooves of the hosts. The point of attachment was located anteriorly, where the free flagellum—no trace of which was evident—normally originates. There were from one to three rows of motionless flagellates along each groove, the individuals often being packed so closely together that they overlapped one another like roofing tiles, their bodies making an angle of some 30° with that of the host. *P. curvicauda* was the dominant plankter in the station, a water butt, as well as in a second station, a hyacinth pond, in which the same phenomenon was noted from the moulted exuviae of belostomatid bugs, but not from mosquitoes. Attached and motionless individuals soon became active on the microscope stage. Once detached from the anchorage they rapidly developed a free flagellum and became indistinguishable from their free living counterparts.

Trachelomonas hispida (Perty) (*2*)

Mosquitoes infested.—*An. hyrcanus, An. kochi, C. t. siamensis.*

Occurrence elsewhere.—A common plankter.

Ref. Kudo (1954) and Laird (1956a) for morphology. A few non-flagellated individuals were seen adhering to larvae of the mosquitoes indicated.

Mastigophora/Protomonadina/Phalansteriidae

Phalansterium digitatum Stein (*1*)

Mosquitoes infested.—*An. kochi, C. annulus.*

Other substrates.—Lemnaceae, *Pistia.*

Colourless individuals, having a single flagellum and measuring 14.3-18.1μ × 3.9-5.3μ (av., 16.3μ × 4.8μ), are located towards the ends of the branches of dendriform, gelatinous colonies. The identification is based on the brief description in Kudo (1954), the colonies closely resembling those figured by Stein (reproduced as Figure 22 of Calkins, 1933).

Mastigophora/Protomonadina/Bodonidae

Pleuromonas jaculans Perty (*3*)

Mosquitoes infested.—*An. kochi, C. fuscocephalus, C. t. siamensis.*

Occurrence elsewhere.—Common in polysaprobic waters, readily attaching itself to all kinds of substrates—even to the cover slip during the microscopical examination of pond samples.

An active little biflagellate, having a naked and usually somewhat amoeboid body measuring 6-10μ × 5μ, and anchoring itself to various substrates by means of the trailing flagellum (Kudo, 1954).

Ciliata/Peritricha/Epistylidae

Epistylis lacustris Imhoff (*19*)

Mosquitoes infested.—*An. hyrcanus, An. kochi, A. albopictus, F. metallica, C. annulus, C. bitaeniorhynchus, C. fuscanus, C. fuscocephalus, C. pseudovishnui, C. t. siamensis.*

Other hosts.—Rotatoria, Cladocera, Copepoda, larval Tendipedidae, etc.

For present purposes the designation *E. lacustris* Imhoff is applied to epistylids forming colonies of 2-46 individuals on dichotomously branched stalks, exhibiting the forms *rhabdostyloides, dichotoma, typica* and *rugosa* as described by Kahl (1935), having zooids 50-75μ long with an elongate Σ-shaped macronucleus, and occurring as epibionts on microcrustaceans and various insects, notably mosquitoes. This ciliate is frequently found on larval mosquitoes in the South Pacific (Laird, 1956a). Roux (c.f. Stiller, 1942) recorded the closely related *E. nympharum* Engelmann from mosquito larvae in Switzerland, Kahl (1935) referred to the occurrence of *E. umbilicata* Claparède and Lachmann on these hosts, and Nenninger (1948) described *E. anophelis* from larval *Anopheles* sp. It is likely that *E. anophelis* is a synonym of *E. umbilicata,* and data published by Stiller (1942) and Sommer (1951) suggest that *E. lacustris* may eventually fall as a synonym of *E. nympharum.*

Pyxidium invaginatum Stokes (*1*)

Mosquito infested.—*C. t. siamensis.*

Other substrates.—Lemnaceae.

This ciliate has a short stalk (best seen when the contractile zooid is fully extended) which telescopes into the posterior part of the body. The peristome is not constricted from the body proper, and the frontal disc is borne on a trumpet-shaped style. The horseshoe-shaped macronucleus is transversely positioned at about the posterior limit of the anterior third. Fully extended examples measure 50-60μ × 20μ, transverse pellicular striations about 0.8μ apart from one another being

clearly evident by phase-contrast. Singapore specimens agree with Penard's (1922) description of *P. invaginatum*. Besides occurring on *Lemna* it is known from *Sphagnum* and the antennae of *Asellus aquaticus* (Nenninger, 1948).

Ciliata/Peritricha/Vorticellidae

Vorticella convallaria (L.) (*5*)

Mosquitoes infested.—*An. hyrcanus, An. kochi, F. metallica, C. bitaeniorhynchus, C. fuscanus, C. pseudovishnui, C. t. siamensis.*

Other substrates.—Surface scum, Lemnaceae, *Pistia, Eichhornia,* larval Anisoptera and Zygoptera, etc.

A cosmopolitan species, redescribed by Noland and Finley (1931). Its zooids are bell-shaped, the opening of the bell being narrower than in *V. campanula* Ehrenberg. They measure 50-95μ × 35-53μ (av., 77μ × 44μ), and the spasmoneme has thecoplastic granules which are clearly visible by phase-contrast. A characteristic feature is the presence of minute granules of secreted material at the surface of the pellicle, especially on the peristome disc. Singapore material is comparable with that described by Noland and Finley, although the length of the stalk is frequently outside their range of 125-460μ (computed from only five specimens). The stalk of examples from insect larvae is usually less than 125μ in length, while that of individuals attached to vegetation may attain a length of 740μ.

Vorticella microstoma Ehrenberg (*30*)

Mosquitoes infested.—16 of the 22 species dealt with, the exceptions being *An. sundaicus, U. nivipleura, T. uniformis, A. aegypti, Ar. obturbans* and *C. sitiens.*

Other substrates.—Detritus, filamentous algae and other vegetation, larval Plectoptera, Odonata, Coleoptera and Diptera of various families.

Ref. Noland and Finley (1931), Laird (1956a). In my experience *V. microstoma* is by far the commonest epibiont of mosquito larvae. Most of the many records of vorticellids from these hosts undoubtedly concern this species. Infestations are often very heavy indeed, the outline of the abdomen, siphon and anal papillae being lost to view beneath a vestiture of myriads of zooids dense enough to be immediately evident to the unaided eye.

Suctoria/Podophryidae

Podophrya collini Root (Pl. II, Fig. 12) (*1*)

Mosquitoes infested.—*C. fuscanus, C. gelidus.*

Other substrates.—Floating scum, submerged debris.

Normally spherical and of a diameter of 40-50μ, although well fed examples may measure as much as 118μ × 102μ. From 30 to 60 capitate tentacles are distributed over the body surface. There is a large, centrally located macronucleus, and a contractile vacuole is present towards the periphery. The stalk is usually about 50μ long, and is attached to the substratum by a basal disc (Root, 1914). *Paramecium caudatum* and *P. aurelia* comprise the chief food of this suctorian, which, according to Root, never exhibits any considerable increase in numbers except in the presence of an abundant supply of one of these ciliates.

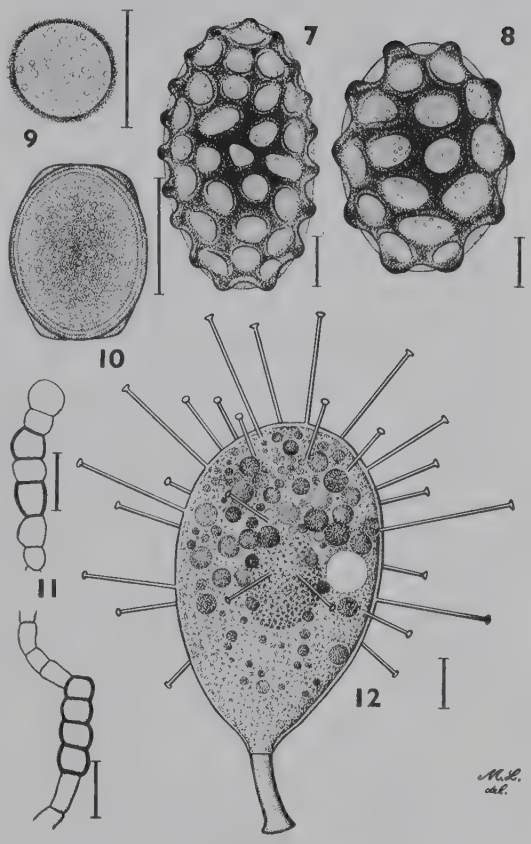

PLATE II

(The scale line at the right of each figure represents 10 microns at the same magnification)

FIGS. 7-9. *Coelomomyces cribrosus,* from larval *Culex tritaeniorhynchus siamensis.* Fresh material, phase-contrast. FIGS. 7 and 8, mature sporangia, 1,200x. FIG. 9, detail of surface depression and pitting, 2,850x.

FIG. 10. *Coelomomyces quadrangulatus* var. *parvus* n. var., from adult *Culex tritaeniorhynchus siamensis.* Fresh material, phase-contrast. Mature sporangium. 2,850x.

FIG. 11. Cells of unidentified member of Fungi Imperfecti, from adult *Culex pipiens fatigans.* Iron haematoxylin. 1,380x.

FIG. 12. *Podophrya collini,* from larval *Culex fuscanus.* Fresh material, phase-contrast. 1,200x.

Examples from rapidly dividing populations at Singapore are more or less spherical and of a diameter of 30-45μ, the stalk being rather longer than the body, except in individuals from mosquito larvae. These are more usually gorged than examples from inanimate substrates, attaining maximum dimensions of 70μ × 45μ. The Singapore *Podophrya* also bears close comparison with *P. fixa* Müller as described by Bhatia (1936) and Liebmann (1951), although Kudo (1954) indicated that the latter species is only 10-28μ in diameter and is thus much smaller than *P. collini*. Most authorities agree that the stalk of *P. fixa* is always shorter than the body. Collin (1912) declared that *P. fixa* selects hypotrichous ciliates as food and absolutely refuses *Paramecium* and other holotrichs. In the light of these data the present species is identified as *Podophrya collini*. This appears to be the first record of a suctorian as a mosquito larval epibiont.

ROTATORIA

Brachionidae

Brachionus rubens Ehrenberg (*4*)

Mosquitoes infested.—*An. kochi, C. t. siamensis, C. annulus.*

Other hosts.—Cladocera, larval Anisoptera.

Small, length 100-170μ size seldom exceeding 120μ × 96μ. Length of spines, 10, 14, 20μ. Ref. Ahlstrom (1940).

ORGANISMS NOT SPECIFICALLY IDENTIFIED

Young, sterile *Oedogonium* filaments were prominent on larval *An. kochi, C. fuscocephalus* and *C. t. siamensis* from two ponds where the same algae were abundant on floatage. An apparently undescribed species of the algal genus *Characium* infested *A. albopictus* larvae from one collection. This organism, which is often abundant on Singapore Cladocera, differs from the two species already known from mosquito larvae—*C. anophelis* Iyengar and Iyengar (1932) and a species close to *C. saccatum* Filarszky recorded by Laird (1956a)—in being elongate-cylindrical to lunate instead of oval to saccate. It sometimes infests the host so heavily that its cells become attached to one another and to the empty walls of cells of earlier generations, occasioning a superficial resemblance to *Sciadium* or *Ophiocytium*.

An undescribed species of *Epistylis* was recorded from two stations, its hosts being *An. hyrcanus, An. kochi* and *C. fuscanus*. Two other peritrichous ciliates were found once each, *Scyphidia* sp. on larval *An. kochi* and *C. t. siamensis*, and *Zoothamnium* sp. on *An. sundaicus* and *C. sitiens* larvae and on decapod crustaceans in the same station, a brackish marsh. The only other epibionts noted were a bdelloid rotifer, common on *A. albopictus* larvae in a tree hole where the same organism was extremely abundant on bottom debris, and a cladoceran. The latter, a species of *Chydorus* recorded from *An. kochi* and *C. gelidus*, was plentiful throughout the station concerned, an *a*–mesosaprobic pond.*

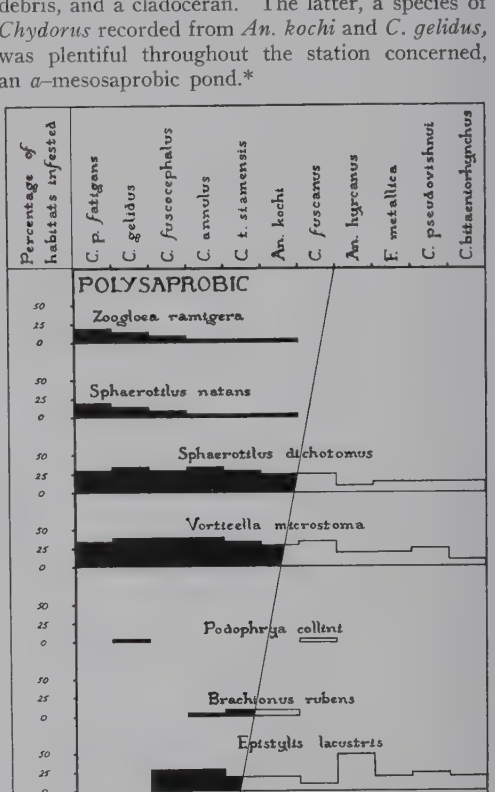

FIG. 13. Correlation of the commoner epibionts with pollution and their mosquito hosts.

LARVAL EPIBIONTS
II. *SIGNIFICANCE*

Had the larvae dealt with been collected without reference to the ecology of their habitats, some at least of their epibionts might well have been regarded as *bona fide* mosquito parasites. In the light of the data presented, though, it is obvious that the larvae concerned had simply become infested with non-specific epibionts characteristic of the habitat and its degree of pollution.

This is illustrated by Figure 13, which correlates the occurrence of epibionts known to be good biological indicators of pollution, with that of

* Epibionts must also be recorded from adults of *T. uniformis*, which frequently bear larval water mites.

surface water mosquitoes recorded from six or more habitats. Thus six of the seven species of Culicidae liable to occur in polysaprobic ponds proved to be the only ones subject to infestation by the sewage bacteria *Sphaerotilus natans* and *Zoogloea ramigera,* which were, however, equally abundant on various submerged objects and on other larval insects in the stations concerned. The abundance of *Vorticella microstoma* and *Sphaerotilus dichotomus* under both polysaprobic and mesosaprobic conditions (Fig. 13), is attested to by the occurrence of these organisms on larvae restricted to one or other of these zones as well as on others able to tolerate various levels of pollution. Likewise, *Podophrya collini* and *Brachionus rubens* both persist from the polysaprobic to the mesosaprobic zone, and infest hosts of similar habits. None of these epibionts exhibited a marked preference for mosquito larvae over other available substrates; neither did *Epistylis lacustris* nor *Vorticella convallaria,* which, being characteristic of mesosaprobic waters, reach their peak of abundance on common mesosaprobes such as *An. hyrcanus.*

Epibionts confined to particular zones of pollution are of some value as biological indicators in mosquito surveys, especially where the larvae concerned have relatively wide limits of tolerance themselves. Thus the occurrence of *Z. ramigera* and *S. natans* upon larvae, combined with the usual macroscopic evidence of the abundance of these bacteria, points to polysaprobic conditions; and flourishing populations of *E. lacustris* and *V. convallaria* are diagnostic of mesosaprobic conditions. *V. microstoma* and *S. dichotomus* are frequently associated with *Z. ramigera* and *S. natans* (Fjerdingstad, 1950, reported that the presence together of the two species of *Sphaerotilus* characterizes polysaprobic waters in Scandinavia), but they may also be found together with *E. lacustris* and *V. convallaria.* Their own wide limits of tolerance thus render *V. microstoma* and *S. dichotomus,* the two commonest epibionts noted, of little value in assessing the degree of pollution. In all cases, it is much sounder practice to base such estimates on general ecological surveys of the habitats concerned.

The occurrence of the less frequently recorded epibionts was usually linked with a prevailing abundance of these organisms elsewhere in the stations in question. Thus the microcrustacean epibionts *Brachionus rubens* and *Colacium vesiculosum* only occurred on mosquito larvae at times when heavily infested Cladocera and Copepoda were very numerous, protozoans normally attached to vegetation and inanimate substrates (*Phalansterium digitatum, Pyxidium invaginatum, Podophrya collini*) were unusually abundant in the stations from which larvae bearing them were collected, and free living organisms (*Streptococcus margaritaceus, Oscillatoria brevis, Phacus curvicauda, Trachelomonas hispida, Pleuromonas jaculans*) sometimes became associated with mosquitoes under similar conditions.

The degree to which particular species of larvae are infested with casual epibionts, largely reflects the frequency of opportunities for contact between the latter and their mosquito hosts. Thus *Podophrya collini* could always be found in a certain pond which fluctuated between the *a*–mesosaprobic and polysaprobic states. Its numbers twice increased very greatly following population peaks of *Paramecium caudatum,* upon which it preys. On both these occasions *P. collini* was recorded from larval *C. fuscanus* and *C. gelidus,* but not from *F. metallica,* the only other species present. All the *C. fuscanus* larvae collected were infested, but relatively few of the *C. gelidus* were. This is explained by the fact that the former, like other *Lutzia* larvae, spend long periods at rest at the surface, lying almost parallel with the surface film, where floating scum provided anchorage for myriads of actively dividing suctorians in the pond concerned. Some of these (never more than nine per individual host) succeeded in attaching themselves to the larval abdomen, abdominal hairs, and thorax. *C. gelidus* larvae, on the other hand, rest in the head-down attitude typical of most members of the genus. This means that a much smaller zone of the body is presented to surface film suctorians, while *F. metallica,* living in association with duckweeds which rarely serve as substrates for *Podophrya,* seldom contact this organism at all.

The nature of the association between free living phytoflagellates and the larval integument, is puzzling—particularly that between *Phacus curvicauda* and its temporary hosts, involving as it did very numerous individuals which completely lost their motility during the period of attachment to mosquito and psychodid larvae and moulted belostomatid exuviae. Gojdics (1953) mentioned records of Euglenidae from the body surfaces of aquatic animals, without further elaboration. None of the other associations involved significant departure from normal behaviour on the part of the organism concerned. However, adjustment to life on a motile rather than a non-motile substratum may be the cause of some minor morphological changes. Mechanical difficulties which long-stalked and non-colonial epibionts face when attached to actively motile substrates, suggest why *Podophrya* and *Vorticella* from mosquito larvae tend to have shorter stalks than those from inani-

nate substrates; and the fact that examples of *Podophrya collini* from larvae tend to be larger than those from surface scum, presumably reflects a higher frequency of fortuitous collisions between the suctorians and their ciliate prey, thanks to larval motility.

These and related matters would repay further study for the fundamental information they are likely to yield concerning a rather neglected route towards parasitism. Heavy infestations with the epibionts flourishing towards the higher levels of pollution may in fact lead to a form of parasitism in the strict sense of the term. The effects of this are, however, intimately bound up with those attributable to prevailing environmental conditions otherwise unfavourable to the mosquitoes concerned. Larvae developing under mesosaprobic conditions and weighed down and grossly impeded in their feeding activities by great masses of epistylid and vorticellid ciliates, may still pupate and give rise to healthy adults (Laird, 1956a). However, a transition to higher levels of pollution, with the consequent advent of unfavourable chemical and physical conditions coinciding with the eclipse of ciliate, phytoflagellate and algal populations by bacteria and saprozoic protozoans, is liable to tip the balance against the mosquitoes. Such a state of affairs may become evident in highly polluted ponds in which heavy growths of vorticellids, *Sphaerotilus* and *Zoogloea* hamper already undernourished larvae. These are thus unable to hold their own in the competition for such suitable nourishment as remains, and they become feebler and more weakly chitinized at each moult. *Sphaerotilus natans* may ultimately invade the cuticular region of such larvae, which die following the destruction of the cells concerned with chitin production. Such an occurrence was first described for *C. p. fatigans* from Shanghai by von Jettmar (1947). Three similar instances, two concerning *C. t. siamensis* and *C. gelidus* and the other *C. p. fatigans*, have been noted at Singapore. The pathogens described by von Jettmar were only identified as "vorticellids" and "streptobacilli," but his data and illustrations leave little doubt that he was dealing with two of the organisms concerned in all three instances at Singapore, *Vorticella microstoma* and *Sphaerotilus natans*.

Endobionts

I. TAXONOMIC

Several endobionts were recorded from the larvae already referred to. *Aspergillus* sp. has only been noticed in old larval cultures at the Department of Parasitology, University of Malaya. Other parasites are reported from adults of *Ar. obturbans* and *C. t. siamensis* (Pasir Panjang, Singapore), *C. p. fatigans* (Dept. of Parasitology, U. of M.) and *T. uniformis* (Bukit Timah, Singapore).

BACTERIA

Schizomycetes/Spirochaetales/ Spirochaetaceae

Borrelia culicis (Jaffé) (Pl. I, Fig. 6) (*3*)

Hosts.—Larval *An. hyrcanus, An. kochi, C. fuscanus, C. gelidus, C. mimulus, C. t. siamensis.*

This spirochaete occurs in the midgut of the host, and measures 5.0-20.2μ × 0.2-0.5μ (av., 11.9μ × 0.3μ) (uncovered Giemsa smears). There is often appreciable tapering towards the ends, and one extremity is usually looped, or curved into the shape of a shepherd's crook (Figure 6). There are from two to six (usually four or five) wavy spirals, 3-5μ in amplitude and 1-2μ in depth.

Jaffé (1907) described a spirochaete from the gut of German culicine larvae under the name of *Spirochaeta culicis*, an un-named species probably identical with this one having already been recorded from Algerian anopheline larvae by Sergent and Sergent (1906). Later records of mosquito spirochaetes from a variety of hosts and widely separated localities were summed up by Sinton and Shute (1939). Jaffé's specimens were 10-20μ long and 0.5μ thick, and had from two to six spirals. Those described by Sergent and Sergent were 8.5-17μ (av., 13.5μ) long, while the ones discovered by Sinton and Shute in the salivary glands of English anophelines ranged from 6μ to 27μ in length (av., about 15.5μ) and had an average thickness of about 0.3μ. The English specimens, like those from Singapore, had from two to six undulations, and the ends were often very distinctly attenuated and looped. The latter feature is certainly of some taxonomic value despite the fact that it is doubtless an artefact attributable to technique.

Bergey restricted the generic name of *Spirochaeta* Ehrenberg to free living spirochaetes characterized by large size and very numerous spirals. He referred relatively small parasitic ones having from three to five wavy undulations to *Borrelia* Swellengrebel. Although Jaffé's spirochaete may have from two to six spirals, its description otherwise fits that of the latter genus, as was recognized by Speer (1927). The Singapore species is accordingly identified as *Borrelia culicis* (Jaffé).

FUNGI

Ascomycetes/Plectomycetes/Aspergillaceae

Aspergillus sp. (*3*)

Host.—Larval *C. t. siamensis.*

The larval alimentary tract was heavily invaded, and spherical fructifications of a brownish colour were sometimes present on the integument of moribund or dead examples. Radiating sterigmata, originating all over the surface of a swollen conidiophore, each bore a single row of conidia of an average diameter of 5μ. These features identify the organism as a member of the genus *Aspergillus* Micheli.

Speer (1927) listed *Aspergillus glaucus* de Bary and *A. niger* van Tieghem from anopheline and culicine larvae. According to Brumpt (1949), the former species has fruiting bodies of a yellow colour, and the latter, having branching sterigmata, is properly referable to *Sterigmatocystis* Cramer. The Singapore species thus differs from those listed from mosquitoes by Speer, but no attempt was made to investigate it further because of a lack of mycological facilities.

Phycomycetes/Blastocladiales/Coelomomycetaceae

Coelomomyces cribrosus Couch and Dodge (Pl. II, Figs. 7-9) (*2*)

Host.—Larval *C. t. siamensis.*

Six of 14 *C. t. siamensis* larvae from a ponded earth drain were parasitized by this *Coelomomyces.* The same collection included 73 *An. kochi* larvae, all of which were uninfected. The fungus was also identified from *C. t. siamensis* larvae sampled during an Army mosquito survey of Blakang Mati Island, off the south coast of Singapore.

Hyphae measuring 6-10μ in diameter were present throughout the body. Yellowish resting sporangia were concentrated in the head capsule, thorax and anal papillae. Sporangia (formalin preserved material) measure 47.2-66.8μ × 31.5-43.0μ (av., 57.0μ × 37.2μ). The wall is 2.5-4.5μ thick, and has a smooth and hyaline inner layer and a sculptured outer layer. Each face has from 11 to 27 circular to elongate-oval thin areas enclosed by ridges (Figures 7, 8). The thin areas are pitted, the apertures being 0.35-0.65μ in diameter (Figure 9). Most sporangia are circular in cross section, and approximately oval in side elevation.

Only one of the known species of *Coelomomyces, C. cribrosus,* has sporangia of this description. The hyphae of this species are 6-11μ thick, the resting sporangia are of the same shape as those under discussion and measure 42-71μ × 24-42μ, and the wall, which is 2.0-4.2μ thick, bears from three to 20 or more pitted depressions on each side (Couch and Dodge, 1947). It is considered that the Singapore species is referable to *C. cribrosus,* which was previously known only from the type locality (Rome, Georgia, U.S.A.), where it parasitizes two species of *Anopheles.*

Coelomomyces quadrangulatus Couch var. *parvus* n. var. (Pl. II, Fig. 10) (*2*)

Host. Adult *C. t. siamensis.*

A well developed mycelium was present in the region of the midgut and the ovaries, the hyphae being 10-17μ thick. The brownish resting sporangia (formalin-preserved material) have a wall 1-2μ thick, and measure 12.9-21.4μ × 8.8-15.6μ (av., 18.1μ × 10.1μ). The thin inner layer of the wall is hyaline, the outer layer being smooth and minutely pitted, the pits averaging 0.35μ in diameter. Four longitudinal ridges give the sporangium a quadrangular appearance in end view (Figure 10).

Couch (1945) described *C. quadrangulata* (the specific name having since been emended to *quadrangulatus* by Couch and Dodge, 1947) from anopheline larvae in Georgia, U.S.A. He gave the thickness of the hyphae as 9.6-25μ, and the measurements of the resting sporangium, which is morphologically similar to that of the present species, as 19-40μ × 12-21μ. Couch drew attention to the fact that the minute pits in the sporangial wall are frequently arranged in rows, recalling the transverse striations of diatom shells. A similar arrangement is sometimes evident in Singapore material. Couch and Dodge (1947) described two varieties of *C. quadrangulatus,* var. *irregularis* from Georgian *Anopheles punctipennis* being of the order of size of the typical variety but having a very irregular and crenellated outer sporangial wall, and var. *lamborni* from Malaya, having sporangia measuring 36-58μ × 26-31μ. Var. *lamborni* was described from the type slide of *Coelomomyces stegomyiae* Keilin, which was almost certainly derived from *A. albopictus,* not from *A. scutellaris* as stated by Keilin (1921) (c.f. Steinhaus, 1946; Laird, 1956a). Couch and Dodge also recorded the typical variety from four species of *Anopheles* in Georgia.

Only one other species of *Coelomomyces, C. pentangulatus* Couch, 1945, has sporangia as small as those of the typical variety of *C. quadrangulatus.* The former species differs from the latter in its much thinner hyphae (4.2-10μ) and in having five or six elevated sporangial ridges. Although the resting sporangia of the present organism are appreciably smaller than those of typical *C. quadrangulatus,* there is otherwise close agreement. *C. quadrangulatus* is already known to exhibit

considerable polymorphism, and to have a wide host range. The Singapore parasite is thus regarded as referable to this species, the unusually small size of its sporangium being recognized by the designation of *C. quadrangulatus* var. *parvus* n. var. The type slide is in the author's collection.

Coelomomyces stegomyiae Keilin (*4*)

Hosts.—Larval *A. albopictus, A. aegypti.*

This species is recorded from *A. albopictus* from three out of 39 stations. All three larval habitats were discarded cans containing fairly clean water of pH 6.6-6.8μ, and lacking any other Culicidae. Sporangia commenced to develop in second instar larvae, the heaviest concentrations being in the head capsule, thorax and anal papillae of old fourth instars. A single fourth instar larva of *A. aegypti* was found to be infected in nature. This mosquito was also the subject of successful laboratory infection experiments, larvae becoming infected when reared in pans of distilled water buffered to an acidity of pH 6.6, into which were introduced dried sporangia derived from parasitized *A. albopictus,* and sediment from the container of the latter.

Resting sporangia measured as follows.—

A. albopictus (Station 1) 29.1-53.4μ × 16.8-29.1μ (av., 40.7μ × 21.6μ)

A. albopictus (Station 2) 30.9-51.2μ × 17.2-27.4μ (av., 42.7μ × 22.1μ)

A. albopictus (Station 3) 34.6-58.3μ × 18.3-30.2μ (av., 44.0μ × 24.1μ)

A. aegypti 32.4-56.1μ × 18.1-28.2μ (av., 40.4μ × 23.2μ)

These figures are compatible with those of Keilin (1921) and Laird (1956a; from Solomon Is. *A. s. scutellaris*), and the smooth sporangial wall with its minute pits 1.3-3.3μ apart has an inner layer averaging 0.7μ thick and an outer one of 1.8μ as described by Keilin.

Unidentified Fungi Imperfecti (Pl. II, Fig. 11) (*1*)

Host.—Adult *C. p. fatigans.*

An adult female of *C. p. fatigans,* incapable of flight, was captured in the Department of Parasitology, University of Malaya. The insect, which bore a mound of a sticky, blackish substance on the mesonotum, died a few hours later. Smears and sections proved that the outgrowth consisted of tangled masses of fungal cells, great numbers of which were also present throughout the alar musculature. These cells (iron haematoxylin preparations) measure 2.8-6.5μ in diameter, single or successive thick-walled ones of a yellowish-brown colour being mixed with thin-walled hyaline ones in linear series (Figure 11). The fungus bears some resemblance to a *Cladosporium* (= *Pullularia*), but as no cultures were made and no further material was discovered it is recognized simply as an undetermined member of the Fungi Imperfecti.

PROTOZOA

Mastigophora/Protomonadina/Trypanosomatidae

Crithidia fasciculata Léger (*9*)

Hosts.—Adult and larval *Ar. obturbans, C. t. siamensis.*

This well known mosquito parasite is recorded from two new hosts. Singapore material agrees with the descriptions of Wallace (1943) and Laird (1956a).

Sporozoa/Gregarinida/Diplocystidae

Lankesteria culicis (Ross) (*36*)

Hosts.—Adult and larval *A. aegypti, A albopictus.*

The smallest trophozoites seen originated from cells lining the larval oesophagus. Examples from this site lack a well developed epimerite, and the smallest one observed measured 11.2μ × 3.3μ (iron haematoxylin preparation). Large, extracellular trophozoites from the lumen of the posterior part of the midgut fall within the size range 150-200μ × 31-41μ given by Ray (1933), and have a prominent epimerite. The darkly staining, conical zone at the anterior extremity of the body, regarded by Ray as a rudimentary protomerite, is clearly differentiated. Ray claimed that the occurrence of these structures, overlooked by some earlier investigators, justifies the transfer of *L. culicis* from the Acephalina (to which the Diplocystidae belong) to the Cephalina. However, as Bhatia (1938) pointed out, the lack of a definite septum precludes this.

Sporozoa/Microsporidia/Nosematidae

Plistophora collessi Laird

Host.—Adult *C. t. siamensis, C. gelidus.*

Approximately one per cent. of *C. t. siamensis* females taken in night catches near Pasir Panjang have their ovaries parasitized by this microsporidian. A detailed description having just been published (Laird, 1959), it is not proposed to discuss it further at this stage.

Ciliata/Holotricha/Frontoniidae

Tetrahymena pyriformis (Ehrenberg) (*3*)

Hosts.—Larval *A. albopictus, C. fuscocephalus, C. gelidus, C. t. siamensis.*

Examples of this organism derived from all four hosts (iron haematoxylin preparations) agree with

MacArthur's (1922) description. Average-sized trophozoites measure some 40μ × 25μ, although examples from populations increasing rapidly by binary fission are appreciably smaller than usual, measuring about 28μ × 18μ, the division forms themselves being some 33μ long and 11μ in diameter at the "waist." Free-living *T. pyriformis* were abundant in the three stations, which were all polysaprobic. Rapidly decreasing populations of cladocerans and rotifers were present in each case. The remains of these animals, likewise moulted exuviae of larval mosquitoes and Tendipedidae in the bottom debris, swarmed with the ciliate, which is already well known as a facultative parasite of various mosquitoes and other aquatic insects (MacArthur, 1922; Wenyon, 1926; Janda and Jírovec, 1937; Muspratt, 1947).

Endobionts

II. *SIGNIFICANCE*

No harmful effects could be ascribed to infections due to *Borrelia culicis, Crithidia fasciculata* or *Lankesteria culicis.* The first two species are known from a wide range of hosts, but the last-named one exhibits a high degree of host specificity. With the exception of Lan-chou Feng's (1933) record from adult *Ar. obturbans,* all published reports of the occurrence of this parasite concern members of the aëdine subgenus *Stegomyia.* All the *A. albopictus* larvae collected from two particular stations during an 18-month period, proved to be infected with *L. culicis,* but associated *Uranotaenia nivipleura* were consistently negative. Attempts to transmit the parasite to the latter mosquito under laboratory conditions, were quite unsuccessful.

Aspergillus sp. may play much the same role in the death of *C. t. siamensis* larvae in laboratory cultures, as *Sphaerotilus natans* sometimes does in nature. Advanced polysaprobic conditions developed in some rearing pans after the addition of unduly large volumes of old hay infusion for feeding purposes, and free living Protozoa had all but disappeared several days before the larvae were ready to pupate. The effects of overcrowding and undernourishment had become marked under environmental conditions less and less suitable for *C. t. siamensis.* Surviving larvae were undersized, weakly chitinized and morphologically abnormal. In many instances the pelt of the preceding larval instar had been retained at ecdysis, and further growth of a weakly chitinized larva within the inadequate space enclosed by a resistant sheath had led to malformation of the siphon and the appearance of circlets of imprisoned setae as described by Langeron (1928). *Aspergillus* sp. enjoyed highly favourable conditions for development following these events, and the larval colonies were rapidly wiped out.

Only three of the mosquitoes studied at Singapore yielded specific and highly fatal pathogens. The death of developing *A. aegypti* and *A. albopictus* infected with *Coelomomyces stegomyiae,* usually takes place before pupation. The same may be said of *C. t. siamensis* and *Coelomomyces cribrosus.* Larvae and adults of Chinese *C. tritaeniorhynchus* are known to be parasitized by organisms viewed by their discoverer (Lan-chou Feng, 1933) as protozoan cysts. The description of these organisms leaves no doubt that they were actually *Coelomomyces* sporangia. Two species may have been involved, one of them being close to *Coelomomyces indiana* Iyengar, but neither *C. cribrosus* nor *C. quadrangulatus* var *parvus* n. var. can be correlated with them. The latter species destroys the entire ovaries of *C. t. siamensis* adults, individual egg follicles of the same host being replaced by the microsporidian, *Plistophora collessi.* It remains to be established whether or not infected mosquitoes go through the motions of ovipositing and in doing so disseminate the infective stages of these parasites. There would seem to be a good chance that they do so in the case of *P. collessi,* the ripe cysts of which roll about freely within the oviducts in fresh preparations.

Further studies of these and other such parasites of adult mosquitoes are called for, not only for the assessment of their significance in population regulation and the possibility of their being utilized as biological control agents, but also because they might prove useful as age-markers in biological studies.

Summary

Larvae of 22 species of mosquitoes yielded numerous epibionts and endobionts, and several parasites of imagines were also recorded. Most of the organisms concerned proved referable to known species. Brief accounts of them are presented for purposes of identification, and *Coelomomyces quadrangulatus* var. *parvus* n. var. is described from the ovaries of adults of *Culex tritaeniorhynchus siamensis.* A microsporidian, *Plistophora collessi,* and fungi of the genus *Coelomomyces* appear significant factors in the natural regulation of their hosts' numbers. *Aspergillus* sp. may be associated with heavy mortality among larvae in laboratory containers allowed to become highly polysaprobic, and heavy multiple infestations with *Vorticella microstoma* and sewage bacteria (*Sphaerotilus natans* and *Zoogloea ramigera*) may kill larvae in nature un-

der parallel conditions of pollution. Associations of organisms serving as biological indicators of varying degrees of pollution are discussed to provide a background for the correct interpretation of the occurrence of larval epibionts, the findings stressing the need for a broader ecological approach to mosquito investigations.

ACKNOWLEDGMENTS

My wife and Mr. C. A. Caldwell undertook most of the field work on which the account of larval parasitology is based. My thanks are due to them and to Dr. D. H. Colless, who supplied the parasitized adult mosquitoes. The rotifer, *Brachionus rubens*, was kindly identified by Mr. C. R. Russell of Christchurch, New Zealand.

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AN INTRODUCTION TO THE CYBERNETICS OF THE ECOSYSTEM: THE TROPHIC-DYNAMIC ASPECT

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In 1942, Raymond Lindeman published his now-classic "trophic-dynamic aspect" of ecology which emphasized the physico-dynamic nature of the ecosystem and pointed up a tendency to ". . . force a 'biological' emphasis upon a more basic functional organization." Since that time there has developed a formal open system thermodynamics (*cf.* Denbigh 1951), certain aspects of which have been applied to the ecosystem (Odum and Pinkerton 1955). Somewhat related to the concept of energy upon which steady state thermodynamics is based are the more subtle abstractions, entropy and information. The study of these physical parameters is the concern of a relatively new discipline, information theory. The theory of information originated from N. Wiener's cybernetics (1948) and the mathematical communication theory of C. Shannon (1948, reprinted: Shannon and Weaver 1949). It has in the short space of a decade found application in many diverse fields, including biology (Quastler 1953; Yockey, Platzman and Quastler 1958). It seems certain even now that further development of the theory will someday permit the description of biological systems in terms of the fundamental processes of control and communication common to all levels of organization.

The present paper is an exploratory attempt to study the ecosystem from a cybernetic point of view, with emphasis on tropho-dynamics. A model of energy flow through a producer-consumer trophic system will be developed as a logical consequence of applying the first two principles of thermodynamics. Then, production rates and efficiency ratios will be formulated from the model and used to compare the organization of several actual communities in such a manner as to be meaningful in terms of the basic principles of order and disorder governing the course of organic evolution.

Physical Entropy and Information

In a statistical sense, all living systems including the ecosystem are highly improbable aggregations of energy (= matter: $e = mc^2$), inherently ordered, and comprising an infinitude of physical and chemical gradients. In contrast to these are non-ordered or random systems which, lacking gradients, can accomplish no work. The disorder of a system is equated in statistical mechanics to its entropy, which is related to the probability distribution of its structural units by the Boltzmann-Planck equation:

$$S = k \ln P \quad , \tag{1}$$

where S is the entropy, k is a natural constant, and P is the number of elementary "complexions" possible, or the *a priori* probability of obtaining a particular quantum orientation from an array of equally probable states. The degree of order in a system is expressed by its information content, defined by Brillouin (1951, 1956) as the negative of entropy (negentropy):

$$I = -S = -k \ln P \quad . \tag{2}$$

Equations (1) and (2) apply only when each complexion is equally probable. In a living system this would not be the case. For such systems, if the number of microstates available is G of m different types:

$$G = \sum_{j=1}^{m} N_j \quad , \tag{3}$$

then for the j-th state the probability is:

$$p_j = N_j / G \quad . \tag{4}$$

The information of a system of G states each with a different probability p_j is:

$$I = GI' = -Gk\sum_{j=1}^{m} p_j \ln p_j \quad , \qquad (5)$$

where $I' = I/G$ represents the mean information per complexion:

$$I' = -k\sum_{j=1}^{m} p_j \ln p_j \qquad (6)$$

(Shannon 1948).

Entropy is usually expressed in entropy units, energy units divided through by Kelvin temperature. Information may also be expressed in entropy units, but the usual unit employed is the *bit,* defined as the quantity of information required to specify a single state in a system whose states may be specified by a binary choice between two alternative events of equal probability. To specify N complexions would require N bits. The physical entropy of such a system, according to Linschitz (1953a) would be:

$$S = k \ln 2^N \quad . \qquad (7)$$

Some estimates have appeared in the literature of the information content of various biological entities which are of interest here to indicate orders of magnitude. For example, Dancoff and Quastler (1953) computed that to specify a single atom in an organism requires no more than 23 bits. Based upon atomic orientation they calculate for a mature man $I \leqq 2 \times 10^{28}$ bits, and based upon orientation of molecules $I \leqq 5 \times 10^{25}$ bits. The information of a germ cell is no more than 10^{11} bits, and that of the whole gene catalogue only about 10^5 bits. Jacobson (1955) has estimated 200 bits to be the minimum information necessary to specify the primordial "organism." Later in this paper calculations will be provided for Silver Springs, Florida based on the work of Odum (1957a) which will indicate that this community consumes about 3×10^{24} bits/cm^2/year of negentropy. As Dancoff and Quastler have observed, the average information content of a printed page is about 10^4 bits, so that it would require 3×10^{20} pages to describe the annual information requirement of the volume under a square centimeter of Silver Springs, which is many orders of magnitude larger than the holdings of the largest library.

What is meant by information "requirement" goes back to Schrödinger's *What Is Life?* (1945), in which is put forth the novel notion that living organisms feed upon negative entropy to compensate for information losses attending the life processes. In Schrödinger's view it is not the energy in food which is important, but only the negentropy. Thus, the ecosystem may be regarded as acquiring negentropy from its environment, storing it as the coded information of its quantum configurations, and (Branson 1953) converting it to enthalpy or entropy as required:

$$\Delta I = \frac{\Delta H}{T} - \Delta S \quad , \qquad (8)$$

where H is enthalpy in energy units, and T is Kelvin temperature. Modern civilization serves as a reminder of the vast quantities of information stored by the great floras of the Carboniferous which only now are being degraded in the process of powering human industry.

Energy Transformations in the Ecosystem

Trophic ecology has traditionally been concerned more with energy flow than with information dynamics so that it seems desirable at this point to relate energy to the statistical definition of information developed above. Thermodynamically the ecosystem is a steady state. Energy enters, is stored or degraded. In the degradation process entropy is created equal in quantity to the energy made unavailable divided by the temperature at which the transformation occurs. The second law of thermodynamics may be formulated to indicate that all natural systems tend to attain a state of thermodynamic equilibrium, in which energy gradients are non-existent and entropy is maximal. Thus:

$$\sum_{j=1}^{m} dS_j > 0 \quad . \qquad (9)$$

The rate of entropy generation by an open system is described in steady state thermodynamics as the difference between power input and output:

$$T\Delta S = J_1X_1 - J_2X_2 \quad , \qquad (10)$$

where J_1 represents input flux under the influence of a force or gradient X_1, and J_2 is output flux associated with X_2 (Denbigh 1951, Odum and Pinkerton 1955). Dividing (10) through by T and rearranging terms, we obtain:

$$\frac{J_2X_2}{T} = \frac{J_1X_1}{T} - \Delta S \quad , \qquad (11)$$

which is analogous to (8). A similar result may be obtained from chemical energetics by dividing the familiar equation for free energy change accompanying reversible chemical reactions,

$$\Delta F = \Delta H - T\Delta S \quad , \qquad (12)$$

through by T:

$$\frac{\Delta F}{T} = \frac{\Delta H}{T} - \Delta S \quad . \qquad (13)$$

Equation (13) is analogous to (8) and (11).

Branson (1953) proposed a law of conservation of information for living organisms which is

the information analogue to the first law of thermodynamics:

$$I_{\text{organism}} = I_{\text{food}} - I_{\text{waste}} \quad . \quad (14)$$

Since I_{waste} is obviously equatable to entropy gain (ΔS), equations (8), (11), (13) and (14) may all be viewed as expressing for particular situations Branson's conservation principle. Extending the principle to the ecosystem, we may write:

$$\left\{\begin{matrix}\text{rate of information change} \\ (\Delta I,\ J_2X_2/T,\ \Delta F/T)\end{matrix}\right\} = \left\{\begin{matrix}\text{negentropy input} \\ (\Delta H/T,\ J_1X_1/T,\ \Delta H/T)\end{matrix}\right\} - \left\{\begin{matrix}\text{negentropy consumed} \\ (\Delta S,\ \Delta S,\ \Delta S)\end{matrix}\right\} \quad , \quad (15)$$

or in terms of energy:

$$\left\{\begin{matrix}\text{energetic output} \\ (T\Delta I,\ J_2X_2,\ \Delta F)\end{matrix}\right\} = \left\{\begin{matrix}\text{energetic input} \\ (\Delta H,\ J_1X_1,\ \Delta H)\end{matrix}\right\} - \left\{\begin{matrix}\text{losses to entropy} \\ (T\Delta S,\ T\Delta S,\ T\Delta S)\end{matrix}\right\} \quad . \quad (16)$$

In what follows the notations of equations (12) and (13) will be employed to describe flow of energy and information through the ecosystem.

Energy Transfer in the Ecosystem

It has been pointed out that the ecosystem, in common with other living systems, degrades energy and in the process generates entropy which, being synonymous with disorder, is incompatible with life. For life to continue, therefore, the entropy created must be dissipated. Branson (1953) has suggested for holozoic organisms that food contains less entropy than metabolic wastes, so that excess entropy is passed off in waste products as well as dissipated directly as heat. In the ecosystem wastes remain for a time, being routed along decomposer pathways and ultimately voided as heat, whence the contained entropy is passed on to the environment to fulfill the second law of thermodynamics, equation (9), with respect to the whole ecosphere (Cole 1958). In this connection the ecosystem may be regarded as an "entropy pump" which employs high grade solar energy to dissipate excess entropy thereby maintaining its physical integrity. This is fully compatible with Schrödinger's notion that life consumes negentropy, the conceptual result being that of a homeostatic system controlled by negative feedback which consumes negentropy to dissipate the entropy generated in the consumption of negentropy. The balance between information gained and entropy created per unit time is of critical significance.

S. Brody, in his important volume on bioenergetics (1945), discussed a model of energy flow through a mammal:

Food (gross energy) →Undigested material
↓
Digested material (digestible energy) →Kidney excretion
↓
Metabolizable energy (ΔH) →Heat increment ($T\Delta S$)
↓
Net energy (ΔF) →Growth and maintenance

in which were employed the notations of equation (12) to designate "metabolizable energy" and its subfractions. A similar flow model may be constructed for the ecosystem with slight modification to take account of the fact that "undigested material" and "kidney excretion" remain in the system as input to decomposer chains. This results in a simplification since only "gross energy," "metabolizable energy," "net energy" and "heat increment" need to be considered for each trophic level.

If "gross energy" is equated to sunlight, then the fraction of incident radiation (Λ) converted to chemical energy in primary production may be designated H_1. At any given time subsequent to the establishment of H_1, some fraction (F_1) will constiute the free energy of the producer trophic level; another fraction will have been converted to entropy (TS_1). The subsequent fate of F_1 is the basis for trophic theory. Employing the conservation principle, a generalized energy flow through the ecosystem may be formulated:

$$\Delta H_1 = \Delta F_1 + \sum_{i=1}^{n} T\Delta S_i \quad , \quad (17)$$

where i refers to trophic level. More specifically, the various pathways by which F_1 may pass through the ecosystem are indicated schematically for a consumer trophic chain in Figure 1. Referring to the figure, a number of parameters may be defined.

The instantaneous rate of organic synthesis by primary producers is dH_1/dt. Similarly, for other trophic levels the rate of energy intake may be represented as dH_n/dt. At all levels beyond producers a fraction ($H_n'_{>1}$) of intake fails to be assimilated and is passed on to decomposer chains. In addition to input to a trophic level by photosynthesis or feeding, energy may also migrate in (imports, H_n'') from outside of the spatial bounds established for study. Of the energy H_n fixed in photosynthesis or ingested at subsequent trophic levels, a fraction TS_n must always be lost to entropy by equation (9). The instantaneous rate of this loss may be regarded as

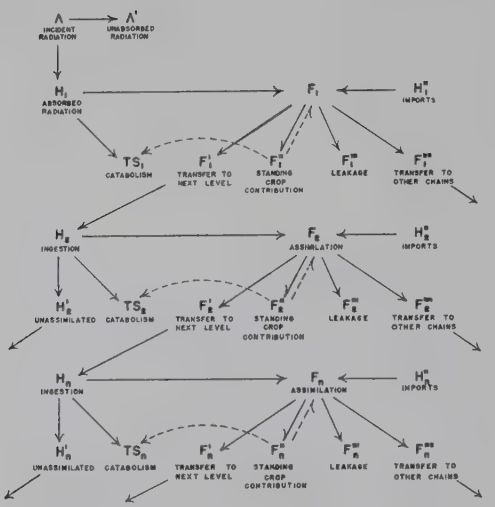

FIG. 1. Schematic model of energy flow through an ecosystem based on the relationship $\Delta H = \Delta F + T\Delta S$. H is analogous to enthalpy, F to free energy, and TS to entropy. The subscripts refer to trophic level. The diagram should not be construed as designating metabolic pathways, but only the energy sources and fates at a time t. Hence, ingested energy (H_n) must be assimilated (F_n) before it is respired (TS_n), although the arrows do not indicate this. Pathways subsequently possible are suggested by the broken arrows.

closely associated with the rate of respiration. This is somewhat objectionable because much of the energy released in respiration is withheld in phosphorylation from direct conversion to entropy. However, since high energy compounds are essentially completely labile over the sampling time usually involved in ecological studies, and since respiration as measured by gas exchange would tend to over-estimate entropy increase thereby providing some correction for negentropy losses in non-respiratory reactions, the energy release of respiration may be equated to entropy gain for the present purposes.

The difference between energy input and losses to entropy and non-assimilation ($[H_n + H_n''] - [TS_n + H_n']$) represents the potential output of each trophic level. The rate of free energy accumulation, assimilation, may be represented as dF_n/dt. Of the energy initially assimilated. one fraction (F_n') is transferred to the next consumer level, another (F_n'') represents contribution to standing crop of trophic level n, a third (F_n''') may be lost from the ecosystem by leakage, and a fourth (F_n'''') is distributed to other trophic chains such as parasites and (upon death) decomposers. As indicated by the broken arrows in Figure 1, portions of the standing crop (F_n'') of a trophic level may become F_n', F_n''', F_n'''' or TS_n subsequent to the point in time represented by the figure.

Now, having rigidly interpreted energy pathways through the ecosystem and having established notations for each point of transfer, it becomes possible to treat the concepts of biological productivity and efficiency with considerable precision and with enhanced significance with respect to physical theory.

PRODUCTION RATES

A general productivity function π_x may be defined for *any* point x of energy transfer in the trophic scheme as some function of time [$\pi_x = f(t)$] such that

$$\lim_{\Delta t \to 0} \Delta \pi_x = 0 \quad , \tag{18}$$

and

$$\lim_{\Delta t \to 0} \frac{\Delta \pi_x}{\Delta t} = \frac{d\pi_x}{dt} = \mathrm{L}, \tag{19}$$

where L is a finite limit.

Numerous productivities have been recognized; some have already been mathematically formulated by Clarke *et al.* (1946).

Hutchinson (*cf.* Lindeman 1942) called the *true* productivity of a trophic level the rate of contribution of energy to the next trophic level ($\Delta F_n'/\Delta t = \Delta H_{n+1}/\Delta t$). Clarke (1946) defined as *gross* production the rate of energy intake ($\Delta H_n/\Delta t$) of a trophic level. Although these two viewpoints are distinct conceptually, in practice they are identical and become incongruous only at the producer level. Odum (1956) has criticized these usages by arguing that there is no process in the higher trophic levels comparable to photosynthesis. This cannot be disputed. However, since the Hutchinson-Clarke definition refers to total input to each trophic level, it appears to be both valid and useful in terms of Figure 1. The Clarke conception of gross production is perhaps somewhat preferable to Hutchinson's true productivity, and it has certainly found wider usage. *Net* production may be represented as $\Delta F_n/\Delta t$, which is the fraction of gross production remaining after respiration ($T\Delta S_n/\Delta t$) and non-assimilation ($\Delta H_n'/\Delta t$). If imports are involved, then net production may include the energy derived from this source ($[\Delta F_n + \Delta H_n'']/\Delta t$).

As indicated in Figure 1, neither gross nor net productivity is directly measurable from standing crop biomass, the latter being a relatively static side issue to the main stream of energy flow. Macfadyen (1948) made this distinction very clear, and physicist Brillouin (1952) recognized it in

relation to the individual organism: ". . . la néguentropie globale de l'individu adulte est supposée constante; et l'on se contente de comparer la néguentropie fournie par les recettes et celle perdue du côté dépenses. L'individu vivant n'entre pas dans le décompte." The change in standing crop over a time interval is $\Delta F_n''/\Delta t$, a derivative to which Clarke (1946) referred as *net increase* or *decrease*. It could also be called *output* productivity to agree with the fact that it represents the change in energy content of a trophic level.

In Table I are assembled energy flow data for several aquatic communities based on the data of Juday (1940: Lake Mendota), Lindeman (1942: Cedar Bog Lake), Teal (1957: Root Spring), and Odum (1957a: Silver Springs). The salient features of the corresponding pathways of each of these ecosystems are readily observable. By summing the appropriate terms at each trophic level in accordance with equation (17), suitably modified, an overall picture of the energy metabolism of each community is obtained. The appropriate modification is:

$$\frac{\Delta H_1+\sum_{i=1}^{n}(\Delta H_i''-T\Delta S_i-\Delta F_i''')}{\Delta t}=\frac{\sum_{i=1}^{n}(\Delta F_i+\Delta H_i'-\Delta F_i''')}{\Delta t} \quad . \qquad (20)$$

Each side of this equality represents *net community output*, the net quantity of energy remaining in the ecosystem as standing crops of organisms and metabolizable detritus and other wastes. In Table II the values for the net outputs of each community represented in Table I are computed. These figures are 357 cal/cm²/yr for Lake Mendota, 82 cal/cm²/yr for Cedar Bog Lake, 370 cal/cm²/yr for Root Spring, and 0 cal/cm²/yr for Silver Springs. The significance of these values will be considered subsequently.

Efficiency Ratios

Efficiency may be defined as the quotient of two general productivities in the trophic scheme, $\Delta\pi_y/\Delta\pi_x$, where $\pi_y = f(\pi_x)$.
Numerous efficiency quotients have been recognized and named, and Odum (1957a) empirically formulated a few which seemed to him most useful. Examples of the variety of ratios possible to obtain may be drawn freely by inspection of Figure 1: $\Delta H_1/\Delta\Lambda$, $\Delta F_1/\Delta\Lambda$, $T\Delta S_1/\Delta\Lambda$, $\Delta F_1''/\Delta\Lambda$, $\Delta H_n/\Delta H_{n-1}$, $\Delta F_n/\Delta H_n$, $T\Delta S_n/\Delta H_n$, $\Delta F_n''/\Delta H_n$, $\Delta F_n'/\Delta F_n$, $\Delta F_n'''/\Delta F_n$, $\Delta H_n/\Delta F_{n-1}''$, and so forth. In addition to these specific ratios for trophic levels, a general efficiency may be computed for the whole community in terms of net output/input. Thus, from equation (17):

$$\left\{\begin{matrix}\text{community}\\ \text{efficiency}\end{matrix}\right\}=\frac{\sum_{i=1}^{n}\Delta F_i}{\Delta H_1} \quad , \qquad (21)$$

and specifically from (20):

$$\left\{\begin{matrix}\text{community}\\ \text{efficiency}\end{matrix}\right\}=\frac{\sum_{i=1}^{n}(\Delta F_i+\Delta H_i'-\Delta F_i''')}{\Delta H_1+\sum_{i=1}^{n}\Delta H_i''}=\frac{\sum_{i=1}^{n}(\Delta H_1+\Delta H_i''-T\Delta S_i-\Delta F_i''')}{\Delta H_1+\sum_{i=1}^{n}\Delta H_i''} \quad . \qquad (22)$$

A theory concerning the efficiency of open systems has been put forth by Odum and Pinkerton (1955), and applied to the ecosystem along with other levels of organization. This is the optimum efficiency-maximum power hypothesis which

Table I. Comparison of trophic level productivities of four ecosystems: Lake Mendota, Wisconsin (Juday 1940); Cedar Bog Lake, Minnesota (Lindeman 1942); Root Spring, Massachusetts (Teal 1957); and Silver Springs, Florida (Odum 1957a). Production is expressed in terms of g-cal/cm²/year

Productivity Parameter	Lake Mendota	Cedar Bog Lake	Root Spring	Silver Springs
ΔH_1	480.0	111.3	71.0	2081.0
$\Delta H_1''$	0.0	0.0	235.0	48.6
ΔF_1	373.0	88.0	300.5	931.9
$\Delta F_1'$	42.0	14.8	230.0	335.8
$\Delta F_1''$	321.0	70.4	0.0	0.0
$\Delta F_1''' + \Delta F_1''$	10.0	2.8	70.5	595.1
$T\,\Delta S_1$	107.0	23.4	5.5	1197.7
ΔH_2	42.0	14.8	230.0	336.8
$\Delta H_2''$	0.0	0.0	1.8	0.0
ΔF_2	26.6	10.4	57.2	147.8
$\Delta F_2'$	2.3	3.1	20.8	38.3
$\Delta F_2''$	24.0	7.0	−0.4	0.0
$\Delta F_2''' + \Delta F_2'''' + \Delta H_2'$	0.3	0.3	36.8	109.5
$T\,\Delta S_2$	15.0	4.4	174.6	189.0
ΔH_3	2.3	3.1	20.8	38.3
$\Delta H_3''$	0.0	0.0	0.0	0.0
ΔF_3	1.3	1.3	11.9	6.7
$\Delta F_3'$	0.3	0.0	0.0	2.1
$\Delta F_3''$	1.0	1.3	−0.4	0.0
$\Delta F_3''' + \Delta F_3'''' + \Delta H_3'$	0.0	0.0	12.3	4.6
$T\,\Delta S_3$	1.0	1.8	8.9	31.6
ΔH_4	0.3	0.0	0.0	2.1
$\Delta H_4''$	0.0	0.0	0.0	0.0
ΔF_4	0.1	0.0	0.0	0.6
$\Delta F_4'$	0.0	0.0	0.0	0.0
$\Delta F_4''$	0.1	0.0	0.0	0.0
$\Delta F_4''' + \Delta F_4'''' + \Delta H_4'$	0.0	0.0	0.0	0.6
$T\,\Delta S_4$	0.2	0.0	0.0	1.3

TABLE II. Calculations of net community output, as defined in equation (20), for Lake Mendota, Cedar Bog Lake, Root Spring and Silver Springs. The figures represent g-cal/cm^2/year

Parameter	Lake Mendota	Cedar Bog Lake	Root Spring	Silver Springs
$\Delta H_1+\sum_{i=1}^{n}\Delta H_i''$	480.0	111.3	558.6	2129.6
$\sum_{i=1}^{n}\Delta F_i$	356.8	82.2	369.6	250.0
$\sum_{i=1}^{n}T\Delta S_i$	123.2	29.1	189.0	1879.6
$\sum_{i=1}^{n}\Delta F_i'''$	0.0	0.0	0.0	250.0
$\Delta H_1+\sum_{i=1}^{n}(\Delta H_i''-T\Delta S_i-\Delta F_i''')$	356.8	82.2	369.6	0.0

claims that steady states tend to operate at low efficiencies which are optimum for maximum output of power. The efficiency ratio upon which this generalization is based is an overall output/input, such as equations (21) and (22) in the situation above. In subsequent work, H. Odum (1956, 1957a, 1957b; Odum and Odum 1955) has suggested that the hypothesis is supported for ecosystems by the characteristically low efficiencies of primary production observed for several communities. Such a conclusion is questionable, however, because primary productive efficiency is not *overall* output/input for the simultaneous functioning of all trophic levels, but is only the efficiency of photosynthesis in terms of the total available solar energy:

$$\left\{\begin{matrix}\text{efficiency of}\\ \text{primary production}\end{matrix}\right\}=\frac{\Delta H_1}{\Delta \Lambda} \quad . \quad (23)$$

Equations (21) and (23) are not equivalent so that the theory of Odum and Pinkerton as it relates to community efficiency cannot be supported on the basis of photosynthetic efficiencies alone. If the whole community is considered, there actually appears (see later, Table IV) a considerable range of output/input possible. In fact, it would appear that the degree of adjustment of a community to its environment, or its nearness of approach to dynamic equilibrium, is inversely related to its overall output/input. Odum and Pinkerton have themselves spelled out why this should be true: "In an ecological community that is growing . . . there is a net increase that can be considered as output power . . . . When the community has passed through its ecological stages of succession and has reached that steady state described by ecologists as climax, *there is no net output* . . . [since] all the energy coming into the community is completely used by leakage and maintenance." (italics mine)

In Table III, data for various efficiencies of the trophic levels of Lake Mendota, Cedar Bog Lake, Root Spring and Silver Springs are presented. Overall community efficiencies are calculated in Table IV. These are: 74% for Lake Mendota and Cedar Bog Lake, 66% for Root Spring, and 0% for Silver Springs.

INFORMATION DYNAMICS

The data of Tables I-IV describe the energetics of each community represented, but provide no clue to how much each departs from the random ideal of the second law of thermodynamics nor whether order is gained, lost, or unchanged in the time involved. It has previously been pointed out that the balance between negentropy gained and entropy generated in a given period is extremely important. An ecosystem may be considered (1) in dynamic equilibrium if the negentropy gained is equal to positive entropy created, (2) in positive information balance if gains exceed losses, and (3) in negative balance if losses exceed gains. These three conditions may be represented by:

$$\frac{\Delta H_1}{T}+\sum_{i=1}^{n}\frac{\Delta H_i''}{T}=\sum_{i=1}^{n}\left(\frac{\Delta F_i'''}{T}+\Delta S_i\right) \text{ (equilibrium)} \quad (24)$$

$$\frac{\Delta H_1}{T}+\sum_{i=1}^{n}\frac{\Delta H_i''}{T}>\sum_{i=1}^{n}\left(\frac{\Delta F_i'''}{T}+\Delta S_i\right) \text{ (positive balance)} \quad (25)$$

$$\frac{\Delta H_1}{T}+\sum_{i=1}^{n}\frac{\Delta H_i''}{T}<\sum_{i=1}^{n}\left(\frac{\Delta F_i'''}{T}+\Delta S_i\right) \text{ (negative balance)} \quad (26)$$

As discussed earlier, information is related both to thermodynamics and statistical mechanics. Because of its relationship with thermodynamics, information balance reflects to what extent a living system is developing, declining or remaining unchanged in its ontogeny in the sense that a positive balance would imply addition of energy-matter, and so forth. In considering the plausibility of information conservation, Branson (1953) suggested that information should be considered the basic parameter for describing living systems. The rationale here would include the fact that information is the antithesis of entropy, just as organic evolution is antithetical to the general evolution of the cosmos at large (equation (9); see also Lotka 1925). Organic evolution proceeds in a direction of increasing information:

$$\sum_{j=1}^{m} dI_j > 0 \quad . \qquad (27)$$

Defined in this way, evolution implies increased order and organization, which are the statistical attributes of information.

It would seem that a full knowledge of the information content of a living system would be equal to fully describing unambiguously the position of the system on an evolutionary scale. However, negentropy may be coupled in diverse ways to produce an organism and, while information content may determine organizational level in a quantitative sense, there is also a qualitative aspect about organization which is an attribute of the pattern of coupling exclusive for each species. Thus, a cell of *Bacterium pycnoticus* contains about 10^{13} bits (Linschitz 1953b) compared to about 2×10^{28} bits for a man. It would be ludicrous to suggest that 2×10^{15} cells of *B. pycnoticus* are evolutionarily equivalent to a human even though cumulatively they possess the same amount of order. The recent article by Bray (1958) should be consulted for a treatment of the distinction between order and complexity. The difference is associated with the handling of statistical information by different organisms, specifically in the conversion to semantic information.

At the present time, there is no way to determine the information content of a living unit at a particular moment. The values of Dancoff and Quastler (1953) given earlier are only crude mathematical estimates and Linschitz' value for the bacterial cell was computed from CO_2 uptake. Somewhat less problematic is the determination of information balance because of the formal equivalences which exist between thermodynamics and statistical mechanics. The temperature at which an energy transformation occurs must be known, however, so that information may be expressed in entropy units (energy units divided by degrees). The only community of those discussed above in the sections on energy flow for which this requirement is met is Silver Springs, which is thermostatic (Odum 1957a) at about 296°K. Tabulated in Table V are the values for information flow in entropy units for each trophic level of Silver Springs, and also for the community as a whole. The figures show negentropy input in the amount of 7.20 cal/degree/cm^2/yr, of which 6.35 were converted to entropy and 0.85 were leaked downstream leaving a balance of zero.

TABLE III. Comparison of various trophic level efficiency ratios for Lake Mendota, Cedar Bog Lake, Root Spring and Silver Springs. The figures represent percent efficiency

Efficiency Ratio	Description	Lake Mendota	Cedar Bog Lake	Root Spring	Silver Springs
$\Delta F_1/(\Delta H_1 + \Delta H_1'')$	Efficiency of assimilation	77.7	79.0	98.2	43.8
$\Delta F_2/(\Delta H_2 + \Delta H_2'')$	(except for producers)	64.3	70.3	24.6	43.9
$\Delta F_3/(\Delta H_3 + \Delta H_3'')$		56.5	41.9	57.2	17.5
$\Delta F_4/(\Delta H_4 + \Delta H_4'')$		33.3	—	—	38.1
$T\,\Delta S_1/(\Delta H_1 + \Delta H_1'')$	Energy degradation or	22.3	21.0	1.8	56.2
$T\,\Delta S_2/(\Delta H_2 + \Delta H_2'')$	respiration efficiency	35.7	29.7	75.4	56.1
$T\,\Delta S_3/(\Delta H_3 + \Delta H_3'')$		43.5	58.1	42.8	82.5
$T\,\Delta S_4/(\Delta H_4 + \Delta H_4'')$		66.7	—	—	61.9
$\Delta F_1'/(\Delta H_1 + \Delta H_1'')$	Efficiency of transfer to	8.8	13.3	75.1	10.8
$\Delta F_2'/(\Delta H_2 + \Delta H_2'')$	next level in terms of	5.5	21.0	9.0	11.4
$\Delta F_3'/(\Delta H_3 + \Delta H_3'')$	ingested energy	13.0	0.0	0.0	5.5
$\Delta F_4'/(\Delta H_4 + \Delta H_4'')$		0.0	—	—	0.0
$\Delta F_1'/\Delta F_1$	Efficiency of transfer to	11.5	16.8	75.4	36.1
$\Delta F_2'/\Delta F_2$	next level in terms of	8.7	29.8	36.2	25.9
$\Delta F_3'/\Delta F_3$	assimilated energy	23.1	0.0	0.0	31.3
$\Delta F_4'/\Delta F_4$		0.0	—	—	0.0
$\Delta F_1''/(\Delta H_1 + \Delta H_1'')$	Efficiency of conversion	66.9	63.3	0.0	0.0
$\Delta F_2''/(\Delta H_2 + \Delta H_2'')$	to standing crop in	57.1	47.3	0.0	0.0
$\Delta F_3''/(\Delta H_3 + \Delta H_3'')$	terms of ingested energy	43.5	41.9	0.0	0.0
$\Delta F_4''/(\Delta H_4 + \Delta H_4'')$		40.0	—	—	0.0
$\Delta F_1''/\Delta F_1$	Efficiency of conversion	86.1	80.0	0.0	0.0
$\Delta F_2''/\Delta F_2$	to standing crop in	90.2	67.3	0.0	0.0
$\Delta F_3''/\Delta F_3$	terms of assimilated	76.9	100.0	0.0	0.0
$\Delta F_4''/\Delta F_4$	energy	100.0	—	—	0.0
$\Delta F_1'/(\Delta H_1 + \Delta H_1'')$	Efficiency of transfer to	8.8	13.3	75.1	10.8
$\Delta F_2'/(\Delta H_1 + \Delta H_1'')$	each level in terms of	0.5	2.8	6.8	0.9
$\Delta F_3'/(\Delta H_1 + \Delta H_1'')$	original input	0.1	0.0	0.0	0.1

TABLE IV. Calculation of overall community efficiencies for Lake Mendota, Cedar Bog Lake, Root Spring, and Silver Springs. The ratios are expressed as percentages

Efficiency Ratio	Lake Mendota	Cedar Bog Lake	Root Spring	Silver Springs
$\frac{\sum_{i=1}^{n}(\Delta F_i+\Delta H_i')}{\Delta H_1+\sum_{i=1}^{n}\Delta H_i''}$	74.3	73.9	66.2	11.8
$\sum_{i=1}^{n} T\Delta S_i/\left(\Delta H_1+\sum_{i=1}^{n}\Delta H_i''\right)$	25.7	26.1	33.8	88.2
$\sum_{i=1}^{n}\Delta F_i'''/\left(\Delta H_1+\sum_{i=1}^{n}\Delta H_i''\right)$	0.0	0.0	0.0	11.8
$\frac{\sum_{i=1}^{n}(\Delta F_i+\Delta H_i'-\Delta F_i''')}{\Delta H_1+\sum_{i=1}^{n}\Delta H_i''}$	74.3	73.9	66.2	0.0

It would be desirable at this point to be able to equate these thermodynamic units to information of the form of equation (6), but this is not possible because all of the microstates available to Silver Springs cannot be specified and are not equally probable. It is possible, however, to convert to information of the form of equation (2) solely to give some idea of the orders of magnitude whch may be involved. This will be done following, and the values obtained in bits will represent the number of yes-or-no questions coded in the most efficient manner which would have to be asked to specify the change of state of the ecosystem in a year *if* each microstate or complexion were of equal probability. In converting from entropy units to bits equation (7) is employed. The Boltzmann constant, k, is 1.38×10^{-16} ergs/degree. Since energy is here expressed in ergs, it is necessary to convert the productivity data from calories to ergs ($1 \text{ cal} = 4.184 \times 10^7$ ergs). A sample calculation follows:

1) General equation:
$\Delta S_i = k \ln 2^{\Delta N}$
$= (1.38)(10^{-16}) \ln 2^{\Delta N}$
$= (1.38)(10^{-16})(2.3) \log 2^{\Delta N}$
$= (1.38)(10^{-16})(2.3)(\Delta N \log 2)$
$= (1.38)(10^{-16})(2.3)(0.301)\ \Delta N$
2) $T\Delta S_i$ (Silver Springs) $= 1879.6$ cal/cm^2/yr
3) $\Delta S_i = 1879.6/296°\text{K} = 6.35$ cal/degree/cm^2/yr
4) $\Delta S_i = (6.35)(4.184 \times 10^7 \text{ ergs/cal}) =$
2.657×10^8 ergs/degree/cm^2/yr
5) $(2.657)(10^8) = (1.38)(10^{-16})(2.3)(0.301)\Delta N$

TABLE V. Information flow through Silver Springs. Values of ΔI are provided for each point of transfer in the trophic scheme, and overall information balance is also computed for the whole community. The figures represent cal/degree/cm^2/yr

Parameter	(n = 1) Producers	(n = 2) Herbivores	(n = 3) Carnivores	(n = 4) "Top" Carnivores
$\Delta H_n/T$	7.03	1.14	0.13	0.01
$\Delta H_n''/T$	0.16	0.003	0.00	0.00
$\Delta F_n/T$	3.15	0.50	0.02	0.002
$\Delta F_n'/T$	1.13	0.13	0.01	0.00
$\Delta F_n''/T$	0.00	0.00	0.00	0.00
$(\Delta F_n''' + \Delta F_n'' + \Delta H_n')/T$	2.01	0.37	0.02	0.002
ΔS_n	4.05	0.64	0.11	0.004

($\Delta S_{\text{decomposers}} = 1.56$)

Community Information Balance

$\left(\Delta H_1+\sum_{i=1}^{n}\Delta H_i''\right)/T$	7.20
$\sum_{i=1}^{n}\Delta S_i$	6.35
$\sum_{i=1}^{n}\Delta F_i'''/T$	0.85
$\frac{\Delta H_1}{T}+\sum_{i=1}^{n}\left(\frac{\Delta H_i''}{T}-\frac{\Delta F_i'''}{T}-\Delta S_i\right)$	0.0

6) $\Delta N = \dfrac{(2.657)(10^8)}{(1.38)(10^{-16})(2.3)(0.301)} = 2.78 \times 10^{24}$ bits
7) $\Delta S_i = 2.78 \times 10^{24}$ bits/cm^2/yr

This calculation may be considerably shortened by using the relationship derived by Augenstine (1953):

$$I = 0.726\ S \qquad (28)$$

for direct conversion from entropy units. Using this formula, an entropy term for a system of C cal/degree/mole would correspond to 0.726 bits of information per molecule. Hence, multiplication of the data in entropy units (Table V) by $0.726 \times$ Avogadro's number (6.02×10^{23}) gives bits/cm^2/yr. In the example above, 6.35 cal/degree/cm^2/yr $\times$ 0.726 $\times$ (6.02×10^{23}) $= 2.77 \times 10^{24}$ bits/cm^2/yr.

In Table VI are tabulated information flow in bits for each trophic level of Silver Springs and for the community as a whole. The data indicate a total input of negentropy of 3.15×10^{24} bits/cm^2/yr. Of this amount 2.78×10^{24} bits were converted to entropy, leaving a positive balance

of 3.7×10^{23} bits/cm^2/yr. This negentropy does not remain in the community, however, for exactly 3.7×10^{23} bits/cm^2/yr are transported downstream so that the net gain or loss of order is nil and the community is in equilibrium with respect to information balance (equation (24)). If this condition were to prevail year after year, there would be little question that the community would be in sufficiently stable steady state to be considered a climax. Thus, the successional status of an ecosystem (its ontogenetic stage) would seem to be precisely and unambiguously defined by its information balance over a period of time. Climax would correspond to equation (24), succession to (25), and senescence to (26).

TABLE VI. Information flow through Silver Springs. Values of ΔI are provided for each point of transfer in the trophic scheme, and overall information balance is also computed for the whole community. The figures represent bits $\times 10^{-21}$/cm^2/year

Parameter	(n = 1) Producers	(n = 2) Herbivores	(n = 3) Carnivores	(n = 4) "Top" Carnivores
$\Delta H_n/T$	3077.8	498.1	56.6	3.1
$\Delta H_n''/T$	70.4	1.5	0.0	0.0
$\Delta F_n/T$	1376.8	218.6	9.9	0.0
$\Delta F_n'/T$	496.6	56.6	3.1	0.0
$\Delta F_n''/T$	0.0	0.0	0.0	0.0
$(\Delta F_n''' + \Delta F_n'' + \Delta H_n')/T$	880.2	163.5	6.8	0.9
ΔS_n	1771.4	279.5	46.7	2.1

($\Delta S_{decomposers} = 680.3$)

Community Information Balance

$$\left(\Delta H_1 + \sum_{i=1}^{n} \Delta H_i''\right)/T \qquad 3149.7$$

$$\sum_{i=1}^{n} \Delta S_i \qquad 2779.9$$

$$\sum_{i=1}^{n} \Delta F_i'''/T \qquad 369.8$$

$$\frac{\Delta H_1}{T} + \sum_{i=1}^{n} \left(\frac{\Delta H_i''}{T} - \frac{\Delta F_i'''}{T} - \Delta S_i\right) \qquad 0.0$$

SUCCESSION AND CLIMAX

The theory of climax has always occupied a central position in formal synecology, yet it is only recently (*cf.* Whittaker 1953) that a unified concept has begun to take form. Modern notions have progressed toward decreasing ambiguity in defining climax, and decreasing subjectivity in recognizing a climax. The foregoing considerations have postulated a single criterion in terms of information dynamics.

Succession is characterized as progression toward maximum complexity, diversity, productivity and stability (Whittaker 1953). It follows that these features are manifestations of the greater control and communication made possible by higher information content. MacArthur reached a similar conclusion several years ago (1955) with respect to community stability. He considered, from the standpoint of the populations involved in the food web, trophic features contributing to stability and concluded that stability is related to the amount of choice which energy has in passing through the ecosystem. This conclusion was formulated in such a manner that his equation for stability was identical to equation (6), which defines information.

The question arises, since climaxes presumably contain more information than lower seral stages, whether or not any differences are to be expected in the apportionment of this information among the various members of the communities. Margalef (1956) pointed out that the natural dynamics of communities lead to a decrease of mean entropy per individual. This implies an increase in mean negentropy per individual suggesting that more highly developed ecosystems support evolutionarily more advanced organisms, a conclusion not inconsistent with subjective experience.

One of the major problems attending the use of information theory to elucidate community dynamics is measurement. Until this difficulty can be overcome it will be necessary to continue using energy flow as the basis for tropho-dynamic analyses. To illustrate the utility in this regard of the model developed above, let us compare Lake Mendota, Cedar Bog Lake, Root Spring and Silver Springs as functioning ecosystems in terms of their trophic level productivities, net community outputs, and various efficiency ratios (Tables I-IV).

Primary production (ΔH_1) in Silver Springs is in excess of 2000 cal/cm^2/yr, which is four times the rate in Lake Mendota, eighteen times that in Cedar Bog Lake, and about thirty times that observed for Root Spring. In each of these communities except the latter photosynthesis is the primary means of energetic input. The main source of energy to Root Spring is allochthonous entry of materials such as leaves and other plant material ($\Delta H_1''$). The magnitude of this input is surprisingly high, amounting to one-ninth the primary production of Silver Springs.

Of the total energy ($\Delta H_1 + \Delta H_1''$) supplied to the first trophic level of each ecosystem, the per-

centages respired by producer biomasses ($T\Delta S_1$) is variable: 56% for Silver Springs, 22% for Lake Mendota, 21% for Cedar Bog Lake, and only 2% for Root Spring. In Lake Mendota 67% of input is converted to producer standing crop ($\Delta F_1''$); in Cedar Bog Lake this value is 63%, and in Root Spring and Silver Springs it is nil. In Root Spring 75% of input is transferred to herbivores, as contrasted with only 13% in Cedar Bog Lake, 11% in Silver Springs and 9% in Lake Mendota. This is a unique situation resulting from the unique nature of the bulk of the input.

This high efficiency of transfer to herbivores in Root Spring results in an herbivore input which is two-thirds that of Silver Springs even though input to the first trophic level was only one-seventh that of Silver Springs. Hence ΔH_2 is 230 cal/cm²/yr in Root Spring and 340 cal/cm²/yr in Silver Springs. Herbivore respiration ($T\Delta S_2$) is essentially equal in these two communities: 175 cal/cm²/yr for Root Spring and 189 cal/cm²/yr for Silver Springs. Herbivore input amounts to only 42 cal/cm²/yr for Lake Mendota of which 15 cal are respired. The corresponding figures for Cedar Bog Lake: 15 cal input, 4 cal respired. Herbivore assimilation (ΔF_2) is 148 cal/cm²/yr in Silver Springs, 57 cal in Root Spring, 27 cal in Lake Mendota and 10 cal in Cedar Bog Lake. In Mendota 90% of the energy assimilated by herbivores is converted to standing crop ($\Delta F_2''$), while 67% is so converted in Cedar Bog Lake. In Silver Springs and Root Spring, however, the contribution of assimilated energy to herbivore biomass is nil.

Only relatively small fractions of initial input to the second trophic level are passed to carnivores: 6% in Lake Mendota, 9% in Root Spring, 11% in Silver Springs and 21% in Cedar Bog Lake. In relation to the original energy supplied to the first trophic level, the efficiencies of transfer to carnivores are: Lake Mendota 0.5%, Silver Springs 0.9%, Cedar Bog Lake 2.8% and Root Spring 6.8%. Efficiencies of transfer to the fourth trophic level, if one exists, do not exceed 0.1% of the original input to the respective communities.

Thus, in both Lake Mendota and Cedar Bog Lake 74% of input represents net output of the communities in terms of equation (20). Therefore, the energetic basis for the differences in character of these two ecosystems must reside in the absolute amounts of primary production of each. As indicated above, input to Lake Mendota is some four times that to Cedar Bog Lake leading to the conclusion that Lake Mendota, a highly eutrophic body of water, is filling in organically four times more rapidly than the less productive bog lake. It is also significant that Cedar Bog Lake, senescent as a lake, is by no means a declining community by energetic standards since it produces more material than it respires and nets 82 cal/cm²/yr. Since net output is positive for both of these communities, they are in positive energy balance. This implies positive information balance and signifies they are successional in accordance with equation (25). The rate of succession in each case is determined by the degree of positive balance which exists, the direction by natural selection of available microstates (through macrostates).

In Root Spring 66% of input is consigned to net output representing a gain of 370 cal/cm²/yr, which is greater even than that deposited by eutrophic Lake Mendota (357 cal/cm²/yr). It would appear, therefore, that this spring is also in positive balance with respect to information and is a successional community. Its uniqueness, as has already been mentioned, is due to the fact that most of its input derives from plants growing outside of the ecosystem, resulting in exceedingly high efficiency of transfer to herbivores.

Silver Springs stands in sharp contrast to these other three communities. It is more highly productive than any of them, but 88% of what is produced is consumed. The remaining 12%, some 250 cal/cm²/yr, is leaked downstream out of the community resulting in a net output of zero. Therefore, as concluded earlier, this community appears to be in equilibrium with respect to information flow (equation (24)) and may be considered a functional climax so long as it maintains a balance between information intake and conversion to entropy.

Summary

A general theory of ecosystem dynamics is developed from basic considerations of order and disorder as elucidated by modern information theory. Disorder is proportional to entropy; order to information, which is negative entropy. The more information a biological unit possesses, the higher may be considered its state of organization since organic evolution proceeds in the direction of increasing information. This is in opposition to the second law of thermodynamics which militates ultimate absolute disarray of all energy-matter. In accordance with this latter principle, the ecosystem tends to consume itself by its life activities. Entropy is continually created from the information stored. To offset this tendency to lose order the system continually

accumulates negentropy from the environment. The balance between information gained and entropy generated in a unit of time determines the dynamic state of the ecosystem. If more information is accumulated than used, the excess is converted to biomass. Such a condition of positive balance represents a growing or successional stage. If more entropy is generated than information gained, the system suffers a net loss of order and declines, as in senescence. When an exact balance between negentropy gains and losses is achieved, the ecosystem has reached a stable equilibrium with respect to order $\rightleftharpoons$ disorder. Such a condition, sustained, marks climax.

These general principles are formulated in terms of a mathematical model of trophic energetics, and the model is used to analyze several aquatic communities to illustrate the practical benefits of an unambiguous interpretation of tropho-dynamics.

Acknowledgments

I wish to thank Dr. Francis C. Evans and Dr. Howard T. Odum for their comments on the original manuscript, and Professor G. Evelyn Hutchinson for an enthusiastic appraisal which inspired several revisions. Dr. Henry Quastler studied the manuscript carefully, which resulted in the correction of several errors and misconceptions.

The material introduced here is new to ecology, and there is a certain element of doubt concerning its applicability and correctness in every detail. Cyberneticist Wiener (1950) wrote: "I am quite aware that I cannot expect to be right in detail and . . . I may even be wrong in principle. Nevertheless, if I give a device which can be verbally formulated in terms of the concepts belonging to the human mind and the human brain, I shall give a point of departure for criticism, and a standard with which to compare the performance to be expected on the basis of other theories."

It is in this spirit that this contribution is presented.

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ENERGETICS IN *DAPHNIA PULEX* POPULATIONS[1]

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Introduction and Initial Assumption

By combining a numerical theory of predation (Slobodkin 1957) a caloric analysis of individual *Daphnia pulex* (Richman 1958) and experimental data on predation in Daphnia populations it is possible to determine the energy budget and efficiency of laboratory Daphnia populations in fair detail. It will be shown that observed field efficiency data and biochemical efficiency data from the laboratory are compatible and that the entire range of reported efficiency values in the literature simply represents different ways of examining the same elementary biological process.

The experimental procedure consisted of maintaining populations of *Daphnia pulex* in 50 cc of water in the laboratory at a temperature of 14-15°C. These populations were counted every 4 days, dead animals were removed, and the total number of newborn was computed from the difference between successive censuses. A number of animals equal to some constant fraction of the number of newborn was removed every 4 days. In some cases the smallest animals present were removed first and then the stock of larger animals was tapped to make up the appropriate number.

Populations in which this procedure was followed will be referred to as "Young removal" populations. In other cases the largest animals present were removed first. These will be referred to as "Adult removal" populations. In the young removal populations removal rates were set as 50% or 90% of the newborn. In the adult removal populations removal rates were set at 25%, 50%, 75%, or 90%.

The number of newborn was determined as the difference between the number of living plus dead animals present at any given census, and the number of living animals present at the termination of the census and removal procedure 4 days earlier.

By assessing the number of animals missing from the population when no reproduction was occurring it was estimated that approximately 66% of the dead animals were recovered in the young removal populations and 63% were recovered in the adult removal populations. Independent experiments by Armstrong (1959) give an average recovery rate of 66% per 4 days in *Daphnia pulex*.

For purposes of calculation the observed removal rate (F in Table I) was taken as the number of animals removed divided by the total newborn, where the number of newborn was computed as (animals alive and dead at beginning of census at time $t+1$) minus (animals alive at termination of censusing and removal procedure at time t) and the number dead were assumed to equal the observed number dead divided by 66% in the young removal populations or by 63% in the adult removal populations.

The populations received 1, 2, 3, 4, or 5 rations of a water suspension of *Chlamydomonas reinhardi* during each 4 days. The ration was determined photometrically. By haemocytometer counts it was found that a single food ration contained 6.2×10^6 Chlamydomonas cells. Using Richman's figure of 1.308×10^{-6} calories per cell, (Richman 1958) the caloric content of a single food ration was taken as 8.1 calories and will be so used throughout. The populations were kept in the dark, except during counts, so that energy fixation by uneaten Chlamydomonas was negligible.

All Daphnia were divided into the subjective size categories of large and small. The caloric content of the small animals was assumed to equal that of newborn animals as determined by Richman, while the large animals were assumed to have the caloric content of Richman's non-reproductive adult females.

The caloric content of an egg in the brood chamber of an adult female was assumed to equal 1/10th the difference between non-reproductive (or eggless) females and reproductive females (containing more than 6 eggs) as determined by Richman, since 10 eggs per female is a reasonable approximation of the number normally found in the brood pouch of a rapidly reproducing female under conditions of mass culture (Slobodkin 1954). The assumed caloric contents per individual are, therefore: for large animals .11620 calories; for small animals .012275 calories; and for each egg .017751 calories.

Details of the technique are presented in more detail in Slobodkin and Richman (1956) and Slobodkin (1954). The overall population growth patterns were essentially identical with those reported elsewhere (Slobodkin and Richman 1956)

[1] This work has been supported by the Rockefeller Foundation (Ga BMR 5661), University of Michigan Faculty Research Fund (Project 993), and the National Science Foundation (G 4396).

TABLE I. Summary of mean numerical data.

				Number in Residual Population				Number in Yield			
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
Pop.	F	N	F. L.	Large	Small	Total	Eggs	Large	Small	Total	Eggs
1.25A	.19096	82	1	33.756	22.817	57.024	15.448	1.7556	.2072	1.9628	2.0350
1.50A	.4164	72	1	22.1641	16.8464	40.0105	14.6076	3.4857	.2777	3.7634	6.4016
1.75A	.65211	82	1	16.634	14.793	31.817	10.118	4.5729	.8902	5.4631	8.5357
1.90A	.83302	75	1	6.800	6.813	13.613	8.013	3.9997	1.9599	5.9596	5.5590
3.25A	.20027	82	3	96.794	65.049	164.770	34.953	4.6216	.3048	4.9264	6.3405
3.50A	.40884	82	3	74.390	52.403	130.134	35.695	9.0851	.4999	9.5850	15.1700
3.75A	.69726	82	3	32.414	24.146	57.889	13.793	8.9753	.6584	9.6337	17.8530
3.90A	.90148	68	3	4.941	7.074	12.162	7.631	4.7643	2.6764	7.4407	8.5725
5.25A	.21909	82	5	164.750	115.344	284.056	66.609	8.6162	.3703	8.9865	13.9845
5.50A	.43631	82	5	63.354	49.450	112.950	36.233	8.7801	.9146	9.6947	18.3159
5.75A	.68361	82	5	15.057	12.889	28.141	9.916	5.7436	1.8658	7.6094	12.5970
5.90A	.85104	64	5	8.716	10.296	19.058	12.446	6.6533	3.3593	10.0126	14.5253
1.50Y	.4219	82	1	30.422	14.657	45.335	23.766	.1705	5.7926	5.9631	.0363
2.50Y	.4385	82	2	60.823	35.665	97.660	40.239	.0617	11.1974	11.2591	0
2'.50Y	.4344	81	2	56.272	34.150	90.910	55.768	.2500	11.5375	11.7875	.0250
4.50Y	.4351	81	4	120.236	73.412	195.348	68.709	.2125	21.2375	21.4500	.5250
5.50Y	.4426	82	5	153.899	89.036	243.581	86.699	1.6460	22.0852	23.7312	2.4384
1.90Y	.8424	74	1	11.278	3.742	15.060	26.930	.8646	17.6215	18.4861	.5670
2.90Y	.8535	74	2	13.914	4.150	18.146	29.878	1.3419	20.0547	21.3966	.6835
2'.90Y	.8568	68	2	28.405	9.151	37.617	50.715	.7423	34.2726	35.0149	.1211
4.90Y	.8532	68	4	52.012	24.059	76.220	115.277	1.4177	69.8507	71.2684	.2536
5.90Y	.8678	66	5	21.572	10.135	31.737	49.672	.6029	36.1666	35.7695	1.1541
0.1	0	82	1	36.642	29.950	66.641	19.257	0	0	—	0
0.2	0	70	2	66.981	54.499	122.665	37.076	0	0	—	0
0.2'	0	81	2	72.774	53.542	127.316	33.075	0	0	—	0
0.4	0	81	4	146.182	105.481	254.502	55.859	0	0	—	0
0.5	0	82	5	176.216	116.731	294.715	93.896	0	0		

The entries in the columns are:
Column (1)—Code name of the populations.
Column (2)—F, the removal rate estimated from births, deaths and censuses, corrected for decomposition of the dead.
Column (3)—Number of censuses.
Column (4)—Food level, number of feedings in a four day period.
Column (5)—Mean number of large animals in the residual population.
Column (6)—Mean number of small animals in the residual population.
Column (7)—Mean total number of animals in the residual populations. This is the sum of columns (5), (6) and the mean number of males.
Column (8)—Mean number of eggs in the reproductive females of the residual population.
Column (9)—Mean number of large animals in the yield per four day interval.
Column (10)—Mean number of small animals in the yield per four day interval.
Column (11)—Mean total number of animals in the yield per four day interval, the sum of columns (9) and (10).
Column (12)—Mean number of eggs contained in the reproductive females in the yield per four day interval.

and will not be reported in detail here. The discussion will center around the mean values of population size and yield from 22 experimental populations and 5 controls. The number of consecutive censuses available for each population is indicated as N in Table I. Each population from which animals were removed is designated by an initial integer, indicating the food level followed by a 2 digit number representing the *a priori* rate of removal and either an A indicating that adults were preferentially removed or a Y indicating that small animals were selected. For example, population 3.75 A received 24.3 calories of food every 4 days and was subjected to removal of the largest possible adult animals at the rate of approximately 75% of the number of newborn.

The control populations are indicated by zero followed by the food level. For example, 0.2 is the control population which received 2 food rations every 4 days. Note that the pairs 2.50Y and 2'.50Y, 2.90Y and 2'.90Y, and 0.2 and 0.2' were treated identically.

By residual population (or standing crop) is meant the animals that remained in the population after the completion of the censusing and removal process. The animals removed are referred to as the yield. Note that the number of eggs in the brood chambers were counted and summed for each population. In Tables I and II the numerical and caloric means for residual population and yield are indicated for each of the 27 populations.

The males present were added separately to the total residual population. In general, males were not removed as yield but some may be included with the small yield animals.

TABLE II. Summary of caloric contents, energy inputs, efficiencies and replacement rates. The entries in the columns are:

	Caloric Content					Caloric Imput/8.1		Yield Efficiency		R
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Pop.	Res. Pop.	Large	Small	Eggs	Total	Initial estimate	Revised estimate	Food chain %	Net %	%
1.25A	4.48238	.20400	.002544	.03612	.24266	1.03	1.065	3.0	2.0	53.2
1.50A	3.05377	.40504	.003410	.11363	.52208	.878	.9763	6.4	6.6	54.9
1.75A	2.29892	.53137	.010932	.15151	.69381	1.00	.9529	8.7	9.0	61.9
1.90A	1.01605	.46477	.024068	.09867	.58751	.770	.6092	7.3	11.9	63.3
3.25A	12.70263	.53703	.003743	.11254	.65331	3.00	3.015	2.7	2.7	57.6
3.50A	9.96224	1.05569	.006139	.26927	1.33110	2.83	2.898	5.5	5.7	60.0
3.75A	4.32416	1.04293	.008085	.31689	1.36791	2.01	1.824	5.6	9.3	66.5
3.90A	.79826	.55361	.032866	.15216	.73864	1.10	.7234	3.0	12.5	65.7
5.25A	21.79134	1.00121	.004547	.24822	1.25398	5.24	5.296	3.1	2.9	58.8
5.50A	8.61391	1.02024	.011231	.32511	1.35658	2.53	2.737	3.3	6.1	59.1
5.75A	2.08630	.66740	.022912	.22360	.91391	.946	1.128	2.3	10.0	55.5
5.90A	1.36072	.77312	.041252	.25782	1.07219	1.19	1.136	2.6	11.7	61.6
1.50Y	4.14001	.01982	.071133	.00064	.09159	1.00	1.112	1.1	1.0	51.1
2.50Y	8.23412	.00717	.137504	0	.14467	2.20	2.187	0.9	0.8	54.5
2′.50Y	7.95404	.02905	.141681	.00044	.17117	2.03	2.150	0.7	0.8	51.8
4.50Y	16.11339	.02469	.260797	.00932	.29481	4.37	4.273	0.9	0.9	54.9
5.50Y	20.52327	.19127	.271206	.04328	.50576	5.50	5.335	1.2	1.2	59.1
1.90Y	1.83495	.10047	.216392	.01006	.32692	.895	1.172	4.0	3.4	52.5
2.90Y	2.19911	.15594	.246272	.01213	.41434	1.15	1.369	2.6	3.7	55.8
2′.90Y	4.31397	.08625	.420868	.00215	.50927	2.42	2.372	2.1	2.7	60.6
4.90Y	8.38719	.08670	.857767	.00450	.94897	4.81	4.728	2.9	2.5	59.0
5.90Y	3.51314	.07005	.431846	.02049	.52239	2.19	2.276	1.3	2.8	57.6
0.1	4.96799									
0.2	9.12509									
0.2′	9.71317									
0.4	19.30797									
0.5	23.59807									

Column (1)—Code name of the populations.
Column (2)—Caloric content of the mean residual population.
Column (3)—Caloric content of the adult animals in the yield per four days.
Column (4)—Caloric content of the small animals in the yield per four days.
Column (5)—Caloric content of the eggs in the yield per four days.
Column (6)—Total caloric yield per four days, the sum of column s (5), (4) and (3).
Column (7)—Caloric input divided by 8.1 as estimated from equation (2), a revised estimate of the food level.
Column (8)—Caloric input divided by 8.1 as estimated from equation (3) for each population.
Column (9)—Food chain yield efficiency. Each entry is equal to the corresponding entry in column (6) divided by 8.1 times the uncorrected food level.
Column (10)—Net yield efficiency. Each entry is equal to the corresponding entry in column (6) divided by 8.1 times the entry in column (8).
Column (11)—The percent of the protoplasm in the residual populations which is replaced during a four day period. Replacement rate is calculated from equation (7).

Analysis of the Data

Approximate energy consumed

Let P_0 represent the size of a control population, P_F the size of a population from which animals are removed at the rate F. Assume population size to be linearly dependent on food supply at all food levels and removal rates, and also assume that the energetic cost to the population of each animal removed as yield is essentially independent of the age and size of the animals removed. The assumption of linearity is justified by previous studies of Daphnia populations, both in the laboratory (Slobodkin 1954, 1957) and in the field (Borecky 1956) and will be discussed in detail below.

Let:

$$\frac{P_F}{P_0} = \varphi(F)$$

We require that when $F = 0$, $P_F = P_0$ and $\varphi(F) = 1$; when $F = 1$, $P_F = 0$ and $\varphi(F) = 0$. At intermediate values of F, the reproductive rate of P_F tends to compensate for removal of animals so that P_F is a non-linear function of F, with the absolute value of $\frac{-dP_F}{dF}$ increasing as F approaches 1.

A suitable value of $\varphi(F)$, that has the appropriate limits and is in general agreement with the known compensating mechanisms of Daphnia populations is:

$$(1) \qquad \frac{P_F}{P_0} = 1 - \frac{F}{2-F}$$

This equation has been derived elsewhere from empirical population variability data (Slobodkin 1957) and is in reasonable agreement with the observed values of P_F for the young removal populations (Figure 1) but not for the adult removal populations (Figure 2). Note that for the young removal populations the assumption of linearity with food supply is approximately valid for both population size (Figure 1) and yield expressed either as total number of animals (Figure 3) or animals plus eggs (Figure 5).

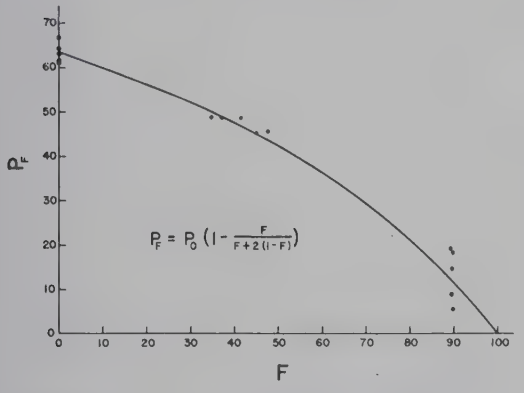

FIG. 1. Young removal populations. Residual population size per unit food supply plotted against F. The line is drawn from equation (1).

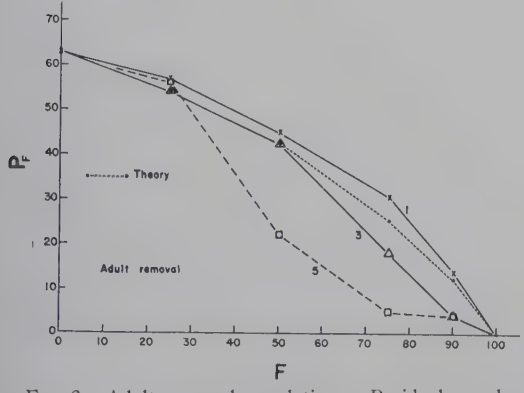

FIG. 2. Adult removal populations. Residual population size per unit food supply plotted against F. The dotted line is drawn from equation (1). The first food level is drawn as —— x ——, the third as —— Δ —— and the fifth as —— □ ——.

Yield and population size are not linearly related to food *supply* in the adult removal populations. Since microscopic examination indicated that Chlamydomonas cells were consistently present in the used medium from populations 3.75A, 3.90A, 5.50A, 5.75A, and 5.90A but not in the used medium from the other populations, it is

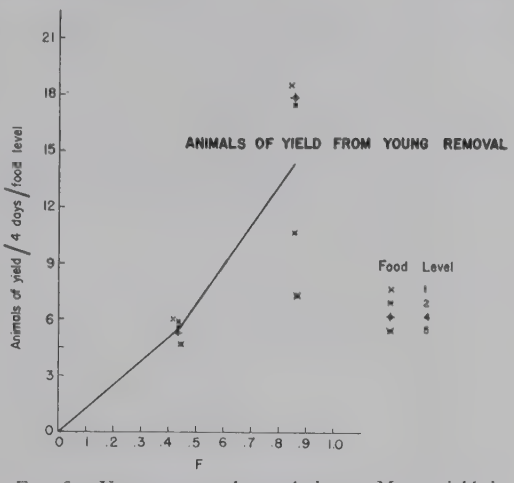

FIG. 3. Young removal populations. Mean yield in animals per census per unit food supply plotted against F. With the exception of populations 2.90Y and 5.90Y, yield per unit food supply seems essentially constant for each value of F.

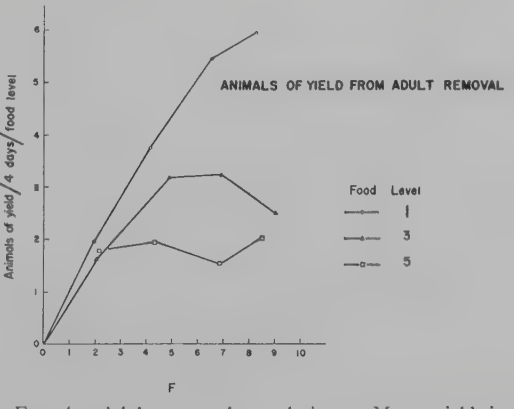

FIG. 4. Adult removal populations. Mean yield in animals per census per unit food supply plotted against F. Yield per unit food supply decreases with food level execept at the lowest values of F. For any given value of F the number of animals in the yield is lower in the adult removal populations than in the young removal populations. The lowest food level populations are indicated by circles, the third food level by triangles and the fifth food level by squares.

clear that in at least some of the populations the food *supplied* was not equivalent to the food *consumed*. There is ample experimental evidence that population size in Daphnia is linearly related to food consumption for the case in which all the food supplied is actually consumed (Slobodkin 1954). We should therefore be able to use the population size to determine the relative food consumption by considering that any deviation from a linear relation between population size and food

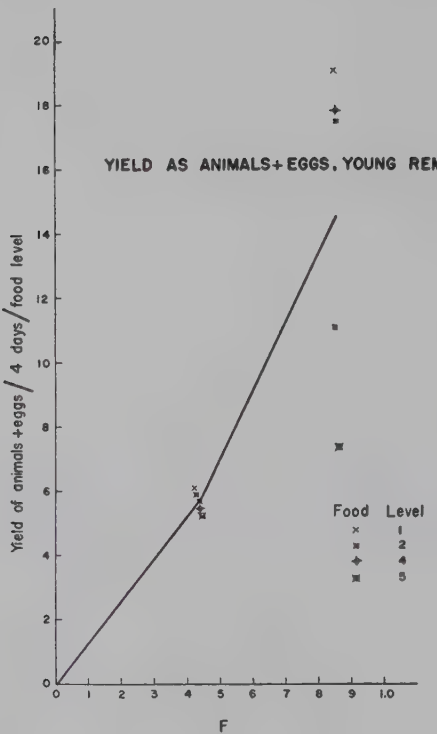

FIG. 5. Young removal populations. Mean yield in animals and eggs per census per unit food supply. The pattern is essentially the same as in Fig. 3.

supply is proportional to the difference between the food supplied and the food actually consumed. It will therefore be assumed that all of the populations are actually following equation (1) but that the food supplied to the population is not necessarily identical with the food ingested by the populations. Analysis of an experimental test of this assumption is now in progress. We will assume that the food consumed by a population is measured by its deviation from the calculated value as determined from F (Table I) and equation (1) according to the following equation:

$$(2) \qquad \frac{P_F}{\text{calculated } P_F} = \text{Food consumed}$$

The calculated food consumed for each population is listed as Column 8 of Table II and is equal to 1/8.1 times the calories consumed, to a first approximation.

If we now replot yield per calculated food consumption level it is found that it is essentially dependent only on F (Figures 7 and 8). Furthermore, if we compute production efficiency (see below) using the food *supply* as our energy input we find negative efficiency values; while production efficiency values derived from the calculated food consumption are all positive and in agreement with other estimates of biological efficiency. That is, failure to use equation (2) leads to nonsense conclusions, while the conclusions derived from equation (2) are simple and in remarkably close agreement with other, independent, data. We therefore consider that the food input derived from equation (2) is a closer approximation to the actual food ingested than is the raw food level data.

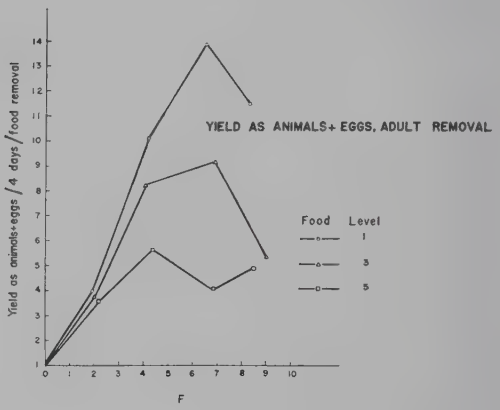

FIG. 6. Adult removal populations. Mean yield in animals and eggs per census per unit food supply. The pattern is essentially the same as in Fig. 4, except that addition of eggs to the yield makes the low food level, adult removal yield comparable in numbers with the young removal yields.

Efficiency

Having values for the caloric content of the yield and the caloric content of the food supplied, the simple quotient (calories of yield divided by 8.1 times food level) is equal to the efficiency with which the Daphnia transform the Chlamydomonas into food for a hypothetical predator. This quantity is listed as Column 9 of Table II. This is the "food-chain"[2] efficiency and is plotted as a function of F in Figures 9 and 10.

Food-chain efficiency increases with F for the young removal populations but has a maximum at intermediate values of F in the adult removal populations. This is simply due to the inability of the greatly reduced residual adult populations to consume all of the food provided. Removal of young does not as severely lower food consuming capacity. The peak value of food-chain efficiency diminishes with increasing food concentration as does the maximally efficient value of F. It might

[2] This term is borrowed, with permission, from a book manuscript by L. C. Cole.

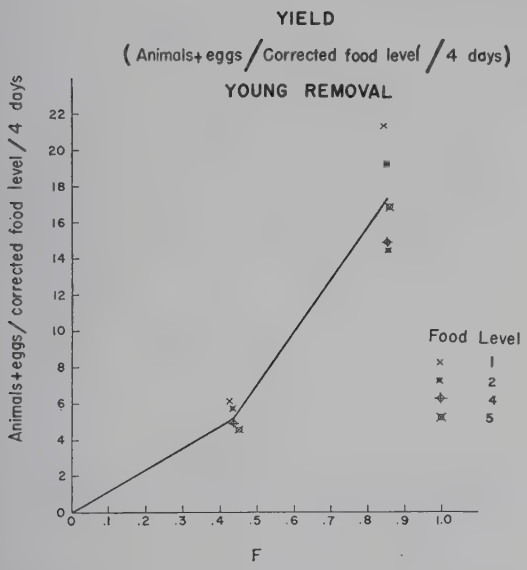

FIG. 7. Young removal populations. Mean yield in animals and eggs per census per unit food consumed as determined from equation (2). Scatter is reduced at high levels of F.

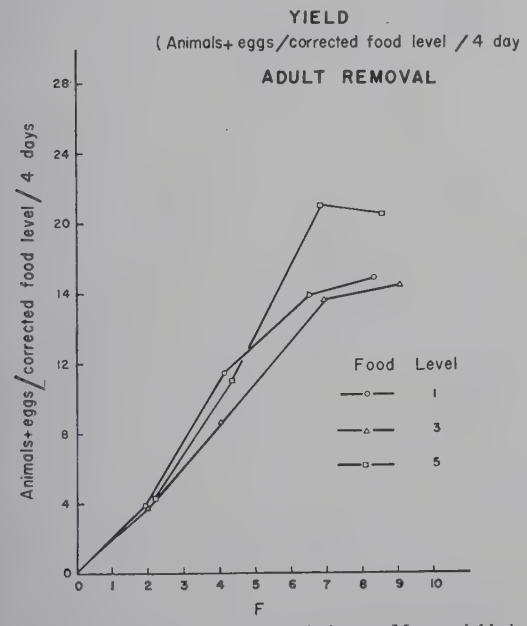

FIG. 8. Adult removal populations. Mean yield in animals and eggs per census per unit food consumed as determined from equation (2). The disparity between food levels has disappeared.

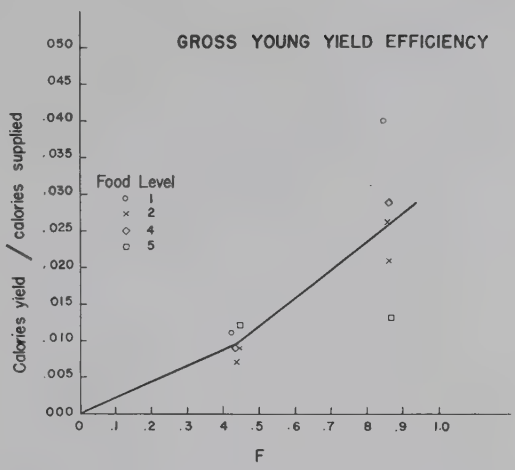

FIG. 9. Young removal populations. Food chain efficiency plotted against F. Food chain efficiency is defined as the total yield in calories divided by the total calories of food supplied to the population.

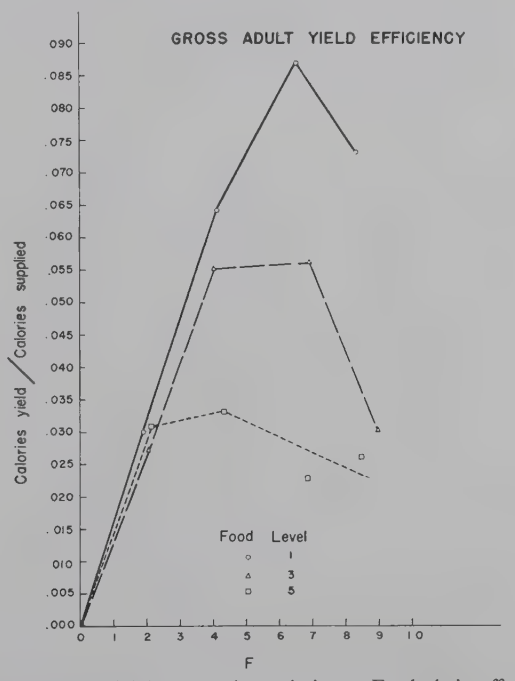

FIG. 10. Adult removal populations. Food chain efficiency plotted against F. At all food levels food chain efficiency has a maximum at some intermediate value of F and the maximally efficient value of F decreases with food level as does the maximum food chain efficiency attained.

be expected, with more dilute algal concentrations, that peak values of 10-12% might be achieved. These values are in general agreement with those reported in nature. (Lindeman 1942, Wright 1958, Juday 1940) It is definitely clear that, if any predator feeds preferentially on young Daphnia, the Daphnia population will not be more than approximately 6% efficient at producing

yield for that predator. In addition to the food-chain efficiency it is of interest to determine the net efficiency, that is, the ratio of calories of yield to calories of food actually consumed. The specific efficiencies of reproduction, growth, and the caloric cost of population maintenance (in calories/4 days/calorie) are also significant.

These will be derived from an analysis of caloric data as follows: The energy budget of a Daphnia population can be written as:

(3) calories of food consumed per 4 days = [(cost, in calories per 4 days, of maintaining each calorie of standing crop) × (the caloric content of the standing crop)] + [(cost per calorie of producing a calorie of yield) × (caloric content of the yield per 4 days.)]

Each of the 22 populations subject to predation must follow equation (3) and for each population we know the caloric content of the steady state population and of the adult, young, and egg yield. We also have an estimate of the calories of food consumed per 4 days. It is therefore possible to solve by least squares for the caloric cost of maintenance and the efficiency of production of adult, young, and egg yield. Details of the solution are presented in the Appendix and Table III. A second approximation to the caloric input to each population is obtained by substituting the best least squares values for the maintenance costs and efficiencies back into equation (3) with the known steady state caloric contents and yields and solving for input. This revised estimate of the calories consumed for each population is listed as Column 8 of Table II.

Using the calculated cost and efficiencies, equation (3) can be rewritten for each population as

$$\text{caloric input per four days} = \frac{\text{caloric content of standing crop}}{\text{.5938 cal. days per cal.}} + \left(\frac{\text{calories of adult yield per 4 days}}{\text{.4830}} + \frac{\text{calories of egg yield per 4 days}}{\text{.06204}} + \frac{\text{calories of young yield per 4 days}}{\text{.03586}} \right) \quad (3)$$

Net efficiency can now be defined as (total calories of yield per 4 days divided by the revised estimate of energy input per 4 days). For the adult removal populations this is a linear function of F, while for the young removal populations there is some indication of higher net efficiency at higher values of F (Figure 11). The lack of complete linearity in the young removal populations is probably due to the fact that a higher proportion of adult animals are removed from these populations at high levels of F. Note that the linearity of net efficiency with F depends on the assumed constancy of the efficiencies and costs. This assumption is supported by other evidence indicating that all quantities in unexploited Daphnia population are linearly proportional to food supply (see especially Slobodkin 1954). If this assumption is not valid there will probably be a slight upward convexity to the relation at high levels of F since our major revision of input calorie estimates occurred at these levels. The values of production efficiency derived from the matrix indicate that if all available energy was utilized for the production of young, new calories of young protoplasm would be produced with an efficiency of 3.6%, the corresponding efficiency for egg production is slightly higher, that is 6.2%. The difference is presumably due to the cost of differentiating the egg protoplasm into a new animal. The efficiency of producing adult protoplasm, in the sense of adding new protoplasm to an extant animal, is 48%, which seems remarkably high at first glance. In particular, the work of Hutchens (1951) would indicate a steady state efficiency of not more than 25-30% for glucose metabolism.

Even more elementary considerations would indicate that an efficiency of more than 30% is

TABLE III. Matrix solution for the values of y and the x_i in equation (4).

	(1)	(2)	(3)	(4)	
	1809.49308530	65.75403750	16.79684106	24.32872472	(1)
A =	65.75403750	6.68031307	1.88140823	.38309611	(2)
	16.79684106	1.88140823	.54208247	.06774019	(3)
	24.32872472	.38309611	.06774019	1.39675661	(4)
	.0013496	−.0509634	.1370824	−.0161774	(5)
A^{-1} =	−.0509634	9.347013	−30.839049	−.1803367	(6)
	.1370824	−30.839049	104.505111	1.0023809	(7)
	−.0161774	−.1803367	1.0023809	.998571	(8)
g_i =	510.16442814	20.44016716	5.28479188	10.098613286	(9)
$\frac{8.1}{x_i}$ =	.207900	.25569	1.98967	3.44231	(10)
	y = .5938	x_1 = .4828	x_2 = .06204	x_3 = .03586	(11)
	y′ = .5938	x_1′ = .4830	x_2′ = .06204	x_3′ = .03586	(12)

The first four rows are the coefficients of equation (4), e.g., the entry in the second column, third row is the sum of the products b_1b_2 for all twenty-two experimental populations where b_1 is the caloric content of the adult yield and b_2 is the caloric content of the egg yield, as indicated in Columns (3) and (4) of Table II. The diagonal elements are the sums of the squares of the caloric data for standing crop (a_{11}), adult yields, (a_{22}), egg yield (a_{33}) etc.

Rows (5) through (8) are the inverse of the matrix consisting of the first four rows.

Row (9) contains the sums of the products of a or the (b_i) multiplied by food level as estimated from equation (2) for each population, e.g., the entry in the third column of row (9) is the sum of the products of columns (5) and (7) in Table II.

Row (10) is the vector resulting from the matrix multiplication of row (9) and the inverse matrix (A^{-1}) rows (5) through (8).

Row (11) contains the initial estimates of y and the x_i values in equations (3) and (4) of the text.

Row (12) contains the values of y′ and x_i′ obtained by substituting the values of y and x_i into equation (3), solving for I and re-computing row (9). The values of I used for getting y′ and x_i′ are listed as Column (8) of Table II.

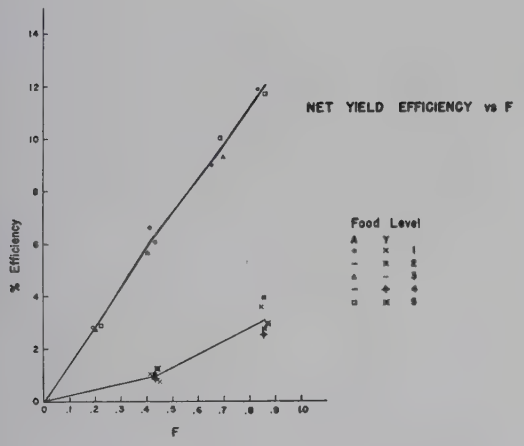

FIG. 11. Net efficiency, all populations. Calories of yield per census divided by the final estimate of calories consumed per census interval (i.e. 8.1 × column 8, Table II) plotted against F. The relation is essentially linear for the adult removal populations and concave upward for the young removal populations.

impossible in a steady state biological system. Consider that at least 150 chemical steps are involved in the complete degradation of any food molecule and that there must be a sufficient number of exergonic steps in the sequence to guarantee unidirectionality of metabolism. The energy burned at each step is unavailable for growth. To leave sufficient residual energy to permit an efficiency of much more than 25% requires an absurdly high mean efficiency per step. The precise value is given by: $n \log e = \log E$ where n is the number of steps, e the mean efficiency per step, and E the overall efficiency of growth. The apparent contradiction is resolved when it is considered that the 48% efficiency value is not a steady state value, since it does not account for maintenance. The effect of removing an animal from a population is twofold. Most obvious is the actual cost of producing the animal. There is also a saving of the energy that would have been required to maintain that animal in the population had it not been removed. The production cost, as determined by the matrix, cannot distinguish between these two effects. Since the cost for maintaining a calorie of protoplasm for 4 days is known (*i.e.*, .5938 cal.) the true efficiency of growth including maintenance costs can be determined.

On the assumption that maintenance cost per calorie is constant, the maintenance cost per 4 days for a single adult Daphnia is $\frac{0.1162}{.5938}$ or 1957 calories. The net cost of removing the same animal from the population is $\frac{0.1162}{.4830}$ or .2406 calories, so that the total cost, for each adult is .4363 calories, and, since the caloric content of each adult is .11620 calories, the true efficiency of growth, taking maintenance into account is 26.63%, which is in agreement with the biochemical requirements.

Corresponding arguments apply to the efficiency of production of eggs and young. Several alternative assumptions are available. We almost certainly must assume that the maintenance cost of eggs is paid by the adult that produced those eggs in its ovary and this is conceivably also valid for young, but because of variations from population to population in the mean number of eggs per adult, we will simply add the maintenance cost to the young and eggs themselves. Owing to the small size of the young and eggs the quantitative effect is negligible, altering cost per animal from .3423 to .3630 calories in the young and correspondingly shifting efficiency from a production efficiency of 3.59% to a true efficiency of 3.38%. Egg costs per egg shift from .2861 to .3160 and the true efficiency of egg growth is now 5.62% rather than the production efficiency of 6.20%.

By using the calculated mean efficiency and maintenance cost values (Appendix, A) and the observed census and yield data from each population it is possible to calculate the rate at which calories are replaced in the residual populations. The details of this calculation are in the Appendix (B). The calculated replacement rates for each population are listed as R in Column 11, Table II. Replacement rate (R) is essentially constant and equal to 57.95%. Richman (1958) measured the weight lost by starved Daphnia and found approximately 56% weight loss in 4 days. To maintain a steady state, replacement would have to be 56% at least from his data. The agreement with the present estimate is so good as to be very surprising. It should be possible to check the theory by calculating the caloric content of the control populations from maintenance cost (y) as estimated from the energy budget, since, in the absence of predation, equation (3) reduces to

$$\text{calories of food consumed per 4 days} = \frac{\text{caloric content of the standing crop}}{\text{.5938 cal. days per cal.}}$$

or

$.5938 \times 8.1 = 4.69$ cal. of standing crop per unit food in the control populations. The observed mean caloric content of the control populations is 4.77.

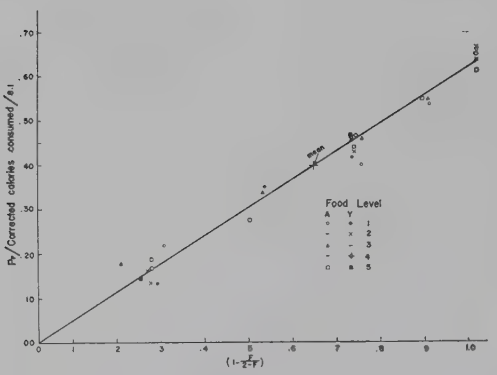

FIG. 12. Residual population size divided by the final estimate of food consumed plotted against $(1 - \frac{F}{2-F})$.

The line has been drawn through the origin and the mean of the points. This is equivalent to Figs. 1 and 2 after re-evaluation of the food consumption for each population.

Note that the control populations influenced the result of the matrix analysis only in the original calculation of energy input from equations (1) and (2).

A similar result is attained if we substitute the mean replacement rate, or Richman's weight loss data from an individual Daphnia for the maintenance cost. That is, we have found 3 numbers that are identical with each other. These are:

1. The percentage weight loss in 4 days by a starved adult Daphnia (56%).
2. The *inverse of* maintenance cost per 4 days per calorie estimated as a weighting constant in an energy budget (59%). (See Appendix A.)
3. The replacement rate per 4 days per calorie estimated on the assumption that all the energy which is not utilized in providing yield is used in replacement reproduction and replacement growth (58%). (See Appendix B.)

As a matter of convenience we have referred to the *inverse of* maintenance *cost* and the replacement *rate* but both concepts are defined in the identical units of *calories per calorie day*. The clear implication is that the same thing has been measured in three different ways. This conclusion is equivalent to stating that the process of maintaining a steady state Daphnia population, regardless of its size (since we have the data from the limiting case of a single animal) consists exclusively of growing or reproducing sufficient new protoplasm to replace the loss in death plus catabolism. This very simple conclusion may be amplified slightly.

It is possible, in principle, to consider the process of maintenance in a biological system in two different ways. We could imagine that there is a certain cost involved in maintaining a mass of protoplasm and that this cost is not related to the growth or reproductive characteristics of the system but in some way is a third property of the system. The other alternative is that growth and reproduction are identical with the processes involved in population increase, size increase of individual animals or production of yield for a predator and are the only processes that are significant in maintenance of a biological steady state.

If the first alternative were correct we would have expected the maintenance cost per 4 days, as determined from the energy budget, to differ from the replacement rate per 4 days as determined from growth and reproductive efficiency data and the census data for each population.

As a matter of fact, maintenance cost and replacement rate are identical. We must therefore conclude that growth and reproduction are identical with steady state population maintenance in Daphnia. An equivalent statement would be that the only direct source of usable energy for metabolic work in a Daphnia population is Daphnia protoplasm and that this protoplasm is produced with a fixed efficiency regardless of its eventual fate.

Possible Second Order Corrections

The surprisingly close agreement between replacement rate per 4 days as calculated and the observed weight loss in starved Daphnia and between observed and calculated control population size indicate that the efficiency values are fairly accurate. It is of particular interest to note that the widely different values that "efficiency" may take in the same system depend on precisely how efficiency is defined.

While the possible sources of error are probably obvious it seems useful to list them here. There may be quantitative inaccuracies in:

1) The original estimate of decomposition rate of dead animals.
2) The assumed caloric contents of the animals and algae.
3) The general assumption of universal linearity.
4) The assumption that both young and adult removal situations ideally correspond to equation (1).

Of these the most important is probably the fourth. Apparently the general agreement of equation (1) with both young and adult removal data is primarily a very fortunate accident. The

cost of young, adults, and eggs are sufficiently close to equality, and the numbers in the yield happen to balance out so that the effect on residual population size is virtually independent of the age and size of the animals removed. By any set of reasonable assumptions it would also be the case that removal of an adult animal from a population reduces the filtering rate of that population considerably more than removal of a young animal or an egg. This is not significant unless the filtering rate is reduced below some critical value. At this point food is left over in the medium. This point will be analyzed in greater detail in connection with another set of experiments. In addition, the efficiency of assimilation tends to vary inversely with food concentration. (Richman 1958) so that even if all the food is eaten there will be effectively lower food absorption at high food levels. These effects are simultaneously compensated for in part by our assumption of the general validity of equation (1). We must concede that equation (1) is not generally applicable to other species and that it should be replaced by a more general statement.

Equation (3) is a general statement in caloric terms. This can fairly readily be translated into numerical terms. A rather complex replacement for equation (1) could then be constructed following the same type of argument as that of Beverton and Holt (1957). It will not be attempted here. Equation (1) is approximately valid whenever the values of efficiency in equation (3) (see Appendix A and Table III) are essentially the same as those observed in Daphnia.

Possible Generalizations and Implications

Growth efficiency of 20-28% may be considered almost universal. Reproductive efficiency equal to slightly less than the square of the growth efficiency may also be very common. The maintenance cost per unit time (y) will tend to vary with the amount of inert material present in the animal's body. For example, the larger the fat depot in the animals the lower will be the replacement rate, resulting in a correspondingly greater reduction in population size as a consequence of removing a single adult animal. The lower limit of production efficiency of adults is approximately 25%. Replacement rate, and caloric content per animal, will vary from species to species. Actual growth efficiency probably will not vary very much. The energetic pattern of a population should then be largely determined from replacement rate, reproductive efficiency and the caloric content of the animals as a function of age.

Conclusions

It is possible to use steady state population data, caloric content data and an assumption of general linearity to determine growth efficiency, both including and not including maintenance cost, and reproductive efficiency. The numerical population equation was primarily significant in permitting us to assess approximate energetic input. In other situations it might be possible to assess energetic input into the population more directly in which case the analysis presented in the matrix (Appendix A) is not dependent on any numerical assumptions whatever and simply depends on caloric content as a function of age or size and on the conditions of the steady state population as far as size distribution and reproductive rate are concerned. The efficiencies determined from the Daphnia data are in surprisingly close agreement with biochemical values (Hutchens 1951) and, depending on the various interpretations that we give to the word efficiency, bracket all existing estimates of ecological efficiency (see Odum 1957 for examples). In essence, we have translated between ecological efficiency in the laboratory, biochemical efficiency determined *in vitro*, and field efficiency values. It would be expected that while replacement rate would vary from species to species the efficiency values for growth and reproduction which we have found will be approximately valid for all animals, or can be used as starting points until better analyses are available. The process of population maintenance in Daphnia is identical with that of replacing existing protoplasm with new protoplasm.

Acknowledgments

The author would like to acknowledge the painstaking work of Miss Mimi Ho in making the actual population counts, the work of Mr. Joseph Armstrong as Research Assistant, and the very valuable discussions with Mr. Joseph Armstrong, Drs. Frederick Smith, Karl Guthe, and Nelson Hairston of the Department of Zoology, University of Michigan, and Dr. Sumner Richman of Lawrence College. I would like to acknowledge Dr. Richman's kind permission to use his caloric content data prior to publication.

Appendix

The calculation of efficiencies, maintenance cost, and replacement rate from caloric content data.

A. Computation of production efficiencies and maintenance cost from an energy budget.

We define the following symbols:

Symbol	*Definition*	*Units*
I	Food calories eaten by the population in 4 days. Input.	cals/time
a	Caloric content of the standing crop of the population, after predation.	cals
b_1	Calories of adults removed by predation per 4 days.	cals/time
b_2	Calories of eggs removed by predation per 4 days.	cals/time
b_3	Calories of young removed by predation per 4 days.	cals/time
1/y	Calories expended per 4 days to maintain one calorie of standing crop.	cal/cal/time
$1/x_1$	Calories expended to produce one calorie of adult yield.	cal/cal
$1/x_2$	Calories expended to produce one calorie of egg yield.	cal/cal
$1/x_3$	Calories expended to produce one calorie of young yield.	cal/cal

For any steady state population we can then write the equation:

$$I = \frac{a}{y} + \left(\frac{b_1}{x_1} + \frac{b_2}{x_2} + \frac{b_3}{x_3}\right) \tag{3'}$$

Note that the symbols enclosed in parentheses in equation 3′ are equivalent to the words enclosed in parentheses in the verbal statement of the energy budget (equation (3) in the text (p. 238)). The constants x_1, x_2, and x_3 have the dimensions of efficiency and are the production efficiences of adults, eggs, and young respectively. That is, if a population did not have to expend energy for its own maintenance and was only producing adults for a predator to remove, it would produce adult tissue with caloric content equal to x_1 times the caloric input and similarly for the production of eggs and young.

We assume that y and the x_i's are constant for all populations. The energy budgets of our 22 experimental populations can each be expressed in the form of equation (3) and these 22 equations can be reduced to a set of four linear equations:

$$\begin{aligned}
\sum_1^{22} aI &= \sum a^a \frac{1}{y} + \sum ab_1 \frac{1}{x_1} + \sum ab_2 \frac{1}{x_2} + \sum ab_3 \frac{1}{x_3} \\
\sum b_1 I &= \sum b_1 a \frac{1}{y} + \sum b_1^2 \frac{1}{x_1} + \sum b_1 b_2 \frac{1}{x_2} + \sum b_1 b_3 \frac{1}{x_3} \\
\sum b_2 I &= \sum b_2 a \frac{1}{y} + \sum b_2 b_1 \frac{1}{x_1} + \sum b_2^2 \frac{1}{x_2} + \sum b_2 b_3 \frac{1}{x_3} \\
\sum b_3 I &= \sum b_3 a \frac{1}{y} + \sum b_3 b_1 \frac{1}{x_1} + \sum b_3 b_2 \frac{1}{x_2} + \sum b_3^2 \frac{1}{x_3}
\end{aligned} \tag{4}$$

which can be solved for the best least squares fit for y and the x_i's. The solution has been done by constructing a 4×4 matrix in which each element a_{ij} is equal to the i, j^{th} coefficient of (4). This matrix was inverted by the Doolittle method and the inverse matrix A^{-1} was then multiplied by the vector with elements

$$g_1 = \sum_1^{22} \frac{aI}{8.1} \quad , \quad g_{i>1} = \sum_1^{22} \frac{b_i I}{8.1} \tag{5}$$

giving $8.1 \times \frac{1}{x_i}$ and $8.1 \times \frac{1}{y}$ directly as $\sum_1^4 g_i a^{i,j}$.

I was taken as predicted from equation (1) i.e., Column 8 of Table II. The matrix, its inverse, the vector and the solution for the x_i and y are presented in Table III. The intermediate calculations have been omitted but the inversion procedure is clearly stated in Anderson and Bancroft (1952), pp. 191-197. Note that equation (3) is a special case of the generalized energy budget:

$$I = \sum M_i C_{m_i} + \sum Y_i C_{y_i} \tag{6}$$

where the M_i's are age, sex or genotype specific categorizations of the calories in the residual population and the $C\ m_i$ the corresponding costs for each category and the Y_i's are categories of yield calories with the $C\ y_i$ the corresponding costs. Equation (3) is used in its present form since analysis of a preliminary set of equations indicated that there was no difference in cost per calorie between the large and small animals in the residual population. The residual calories were therefore pooled and the control populations omitted from the analysis. When the values of y and x_i from the matrix solution are reinserted, for each population, in equation (3) and multiplied by the appropriate constants and summed a new estimate of I is acquired. This new estimate of I for each population is listed as Column 9 of Table II. If the matrix is re-solved, using the new estimate of I, no significant changes occur in our estimates of y and the x_i.

B. Computation of replacement rate (R) from efficiencies, maintenance cost, birth and standing crop data.

The rate at which the caloric content of the residual population is replaced can be computed as follows:

We define R as the replacement rate in calories per calorie per 4 days.

We define β as the caloric content of the newborn produced per four days. This is computed for each population as the difference between the number born and the total number removed as yield multiplied by the caloric content of a newborn animal. Note that it could also be computed as the total number dead of non-predatory causes multiplied by the caloric content of one newborn.

The replacement calories occur as newborn animals (β) and as new protoplasm added to the existing animals, presumably with an efficiency x_1.

The total energy available for replacement is $\frac{a}{y}$.

The total energy available for growth is the difference between $\frac{a}{y}$ and the energy utilized for reproduction $\frac{\beta}{x_3}$. The calories of new protoplasm added by growth in four days are therefore

$$x_1\left(\frac{a}{y}-\frac{\beta}{x_3}\right)$$

and replacement rate for each population can then be computed as

$$(7) \qquad R=x_1\left(\frac{a}{y}-\frac{\beta}{x_3}\right)+\beta=\frac{x_1}{y}-\frac{\beta}{a}\left(\frac{x_1}{x_3}-1\right)$$

All of the terms in equation (7) except for β and a are derived from the solution of equation (4) so that constancy of R from population to population is a measure of the constancy of $\frac{\beta}{a}$. The values of R for each population are listed as Column 11, Table II.

As a matter of fact, $R \approx y$, but this is an empirical agreement and is not analytically determinable from equation (7).

Summary

Twenty-two populations of *Daphnia pulex* were subjected to predation in the laboratory. Five control populations were maintained. The steady state census and yield data and the food consumption of each population were translated into calories by use of conversion constants. Energy budgets were then written for each population by equating energy consumption to weighted caloric content values of the standing crop and yield of adults, eggs, and young. From the 22 energy budgets of the experimental populations, best least squares estimates were made for the weighting constants by a matrix inversion technique.

The weighting coefficients correspond to the respective inverses of the caloric replacement rate in the residual populations and the production efficiencies of adults, eggs, and young.

Efficiency in the various senses of ecological efficiency, production efficiency, and biochemical efficiency were then determined for the Daphnia populations. Each value was in agreement with correspondingly defined efficiency values in other systems. The implication of this agreement is that efficiency is approximately constant from species to species.

The replacement rate per calorie of standing crop was found to be identical with the maintenance cost per calorie of standing crop, implying that maintenance and replacement growth are identical processes.

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BIOLOGICAL CONTROL OF PAMAKANI, *EUPATORIUM ADENOPHORUM*, IN HAWAII BY A TEPHRITID GALL FLY, *PROCECIDOCHARES UTILIS*. 2. POPULATION STUDIES OF THE WEED, THE FLY, AND THE PARASITES OF THE FLY

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Procecidochares utilis Stone, a tephritid gall fly introduced into Hawaii in 1945 to combat *Eupatorium adenophorum* (Spreng.), a rangeland weed, has been highly successful in the control of this plant in some localities but has exerted little control in others. Detailed studies on the progress of the fly, its effects on the plant, and the parasites of the fly were made during 1949 to 1957. The history of the plant in Hawaii, the biology of the fly, its effects on the plant, and the benefits derived from the fly have been treated in a recent paper (Bess and Haramoto 1958). The present paper is concerned with population studies of the weed, the fly, and the parasites of the fly in different localities and seasons, especially on the island of Maui.

METHODS

The locations for obtaining data were selected to include the different vegetation zones (Ripperton and Hosaka 1942) in which pamakani occurs on Maui. The elevations and rainfall of the vegetation zones and the locations of the regular collection sites are shown in Figure 1. Although the bulk of the data were obtained at these regular collection sites on Maui, supplemental data were also obtained from a few other localities on Maui and from the islands of Lanai, Molokai, Oahu, and Hawaii.

When these studies were begun in 1949 it was evident that the fly was being parasitized and that the plants were more heavily galled in some localities than in others. Random collections of galls were usually taken twice a year, spring and fall, from a number of localities to determine the variation in parasitization at different localities and seasons. An attempt was made to collect a sufficient number of galls at each locality to obtain more than 100 individuals per sample. The galls collected were held for emergence of flies and parasites in the laboratory at Honolulu. Although galls and larvae in various stages of development occur simultaneously the samples for rearing records were limited to those which contained

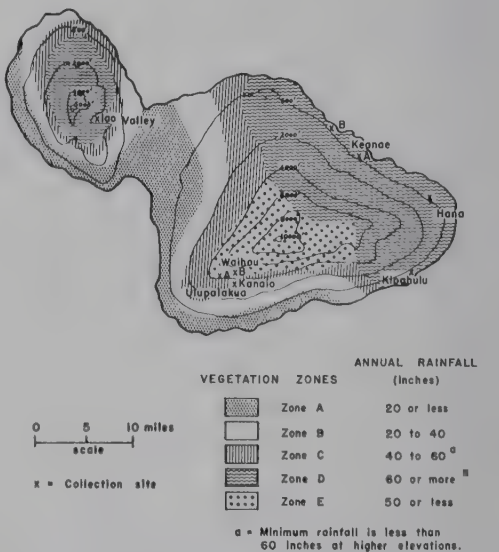

FIG. 1. Map of Maui showing vegetation zones, annual rainfall, elevations, and the locations of the regular collection sites. Map based on information presented by Ripperton and Hosaka, 1942.

"emergence windows." The galls that contained puparia or larvae sufficiently mature to complete their development after the galls had been removed from the plants produced either flies or parasites. Parasitization was calculated on the basis of the emerged adult flies and parasites, all of which were solitary.

At the time of collecting the galls, estimates were made of the proportion of the plants that were galled at each locality. In July of 1957 random samples were taken in certain localities to obtain data on the height of plants, number of main and lateral stems galled, number of galls on the top 6 inches of the main stems, and number of eggs per stem. The number of stems and galls were also obtained within 5-ft. by 5-ft. plots.

Experiments designed to determine the growth rate of infested and non-infested plants were made in the greenhouse. Information on the life history and habits of the fly was obtained from laboratory

[1] Published with the approval of the Director of the Hawaii Agricultural Experiment Station as Technical Paper No. 418.

rearings, field observations, and the dissections of field collected galls.

Data

Bionomics of fly and parasites

The life history and habits of *P. utilis* were discussed in some detail in an earlier paper (Bess and Haramoto 1958); however, its life history is shown here in the graph which illustrates the comparative growth rates of the galled and non-galled plants (Figure 2). Only a list of the parasites was given in our previous paper; therefore, information relative to their biologies and habits which is pertinent to these population studies is presented below.

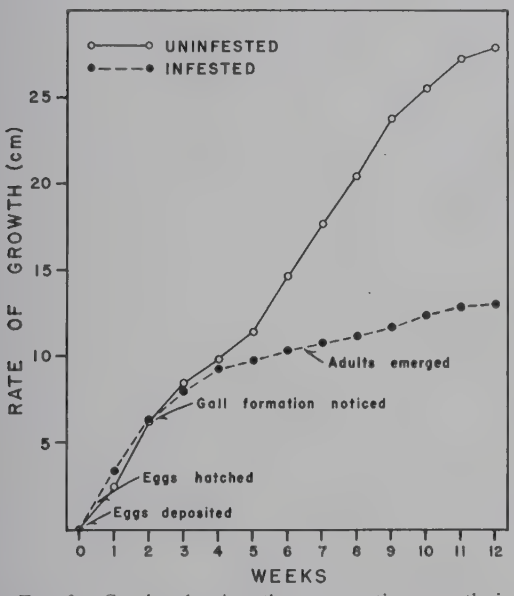

Fig. 2. Graphs showing the comparative growth in height of infested and non-infested plants in the greenhouse and the duration of the developmental period of the fly. The curves are based on 5 plants of each group. The infested plants were galled at a single point.

There were 5 species of hymenopterous parasites [*Opius tryoni* Cameron, *Opius longicaudatus* (Ashmead), *Bracon terryi* (Bridwell), *Eupelmus cushmani* (Crawford), and *Eurytoma tephritidis* Fullaway] reared from *P. utilis* during these studies. The two opiines were imported to combat other tephritid flies but are casual parasites of this fly. Each of the other 3 parasites was abundant in a number of localities on Maui where the major portion of the population data was obtained.

O. tryoni is a braconid parasite which oviposits within nearly mature host larvae and the adults of which emerge from the host puparia. The biology of this species is given by Pemberton and Willard (1918). *O. longicaudatus,* introduced to combat *Dacus dorsalis* Hendel, has habits similar to those of *O. tryoni* (Bess, van den Bosch, and Haramoto 1950). *B. terryi* is an external larval parasite. After becoming fully grown the larva pupates within a silken cocoon inside the cavity of the gall. The species was described from specimens reared from *Tephritidis crassipes* (Thoms.) from *Bidens* sp. in Hawaii (Bridwell 1919). *E. cushmani,* a eupelmid, is an internal larval parasite which completes its development within the puparium of *P. utilis* and the adults of which emerge from it. This parasite was introduced into Hawaii in 1934 (Swezey *et al.* 1939) to combat the pepper weevil, *Anthonomus eugenii* Cano, and which has since been reared also from *Bruchus sallaei* Sharp (Swezey, 1938) and two anthribids, *Araecerus fasciculatus* (De Geer) (Pemberton 1954) and *Araecerus levipennis* Jordan (Fullaway 1956). A few adults of *E. cushmani* were reared from the silken cocoons of *B. terryi,* which indicates that it also acts as a hyperparasite. Because of this habit, the parasitization by *B. terryi* was higher but the total parasitization figures are unaffected by it. *E. tephritidis,* a eurytomid, is an internal larval parasite of *P. utilis.* It usually parasitizes fully grown larvae but occasionally parasitizes smaller larvae. Apparently when the smaller larvae are attacked and consumed before forming puparia, the *E. tephritidis* larvae emerge from the host larvae and pupate outside rather than within the puparia in the usual manner.

Mr. N. L. H. Krauss stated in personal correspondence that he reared the following species of parasites from *P. utilis* during 1944-45 at Cuernavaca, Morelos, Mexico: *Eurytoma obtusiventris* Gahan (Eurytomidae); *Eupelmus cyaniceps* (Ashm.) and *Eupelmus allynii* (French) (Eupelmidae); *Torymus umbilicatus* (Gahan) (Torymidae); *Galeopsomopsis* sp. (Eulophidae); and *Zatropis* sp. (Pteromalidae).

Abundance of pamakani in different localities

Although pamakani is widely distributed on Maui, extensive dense stands are restricted to the higher elevations on the slopes of Haleakala above Ulupalakua and Kipahulu. On Maui localized dense stands are present in Iao Valley and along the Hana coast. Isolated plants and sometimes fairly dense small patches are found here and there in vegetation zones C1, C2, D1, D2, D3, and E1 on all the islands except Kauai (Hosaka and Thistle 1954). Where the fly has been spectacularly successful in bringing the weed under control the plant is becoming sparser and has been completely eliminated over large acreages.

Because pamakani grows in dense stands it was impossible to determine the number of individual plants present, but within measured areas it was possible to count the number of stems or growing points that were available for attack by the fly. It was found that in dense stands there were between 15 and 35 stems per square foot.

Another facet of the pamakani population is the extensiveness of the areas in the general vicinity of Ulupalakua and Kipahulu with pamakani as the dominant cover, while in most of the other localities it occurs sparsely or in patches with other plants making up the dominant vegetation. This means that even though the number of stems per unit area in the Hana coast and Ulupalakua area was about the same, the total area of pamakani was much less in the former. In other words, the over-all food supply or breeding material for the fly was much less in the outlying areas than in the Ulupalakua area.

Abundance of P. utilis

Adults of *P. utilis* were conspicuously numerous in some localities but relatively scarce in others. Hundreds of *P. utilis* adults were observed on the foliage of the native plant known as olopua, *Osmanthus sandwicensis* (A. Gray) Knobl., at Kanaio. On one occasion 168 individuals were collected with two sweeps of an insect net, and on later examination in the laboratory all of them proved to be males. At both Kanaio and Waihou it was not unusual to count upwards of a dozen flies on a few branches of a pamakani plant. On the basis of counts made on pamakani it was evident that thousands of flies were present per acre; however, no attempt was made to obtain estimates of the actual population.

The whitish eggs, which are deposited between the young paired leaves before they unfold at the tip of the growing shoot, were readily found in large numbers at Kanaio and Waihou. In some instance more than 40 eggs were found between a single pair of such leaves. The average number of eggs per 25-stem sample was 167 ± 10^2 at the higher elevation at Waihou (B) and 360 ± 28 at the lower elevation (A), while at Keanae and Iao Valley there were 18 ± 5 and 11 ± 4, respectively. Furthermore, about 90% of the main stems examined from Waihou contained eggs, while less than 20% of those from Keanae and Iao Valley contained eggs.

Infestation was evident from galling, which is the response of the plant to feeding by the larvae. The last-instar larva makes a circular channel, referred to as "emergence window," in the wall of the gall, leaving the thin epidermis intact. Therefore, the number of "emergence windows" serves as an index of the individuals that were successful in completing their larval development. As can be seen in Figure 3, the highest number of galls on the top 6 inches of the main stems occurred at Kanaio where the mean for the 100-stem samples taken at random exceeded 7 galls per stem and the lowest at Keanae where there were only 0.3 gall per stem. Where the *P. utilis* population was low most of the galls were simple galls, and where it was high the majority of the galls were compound ones. At Keanae a high percentage of the paired young leaves at the growing tip that serve as oviposition sites escaped attack. On the other hand, at Waihou and Kanaio more than 80% of such leaves were attacked. Moreover, where there were several eggs per deposition site, most of the galls that developed were compound, and there were more galls per stem (Figure 3). On the basis of these samples the stems were galled as follows: Keanae 36 ± 3, Iao Valley 87 ± 3, Waihou (B) 98 ± 0.4, Waihou (A) 100, and Kanaio 100. These figures also indicate the percentage of the main stems within the samples that had one or more galls. The number of galls per 100 stems was a better index of the gall population: Keanae 51 ± 6, Iao Valley 166 ± 5, Waihou (B) 295 ± 9, Waihou (A) 450, and Kanaio 810. However, this index of the gall population does not give a true picture of the *P. utilis* population

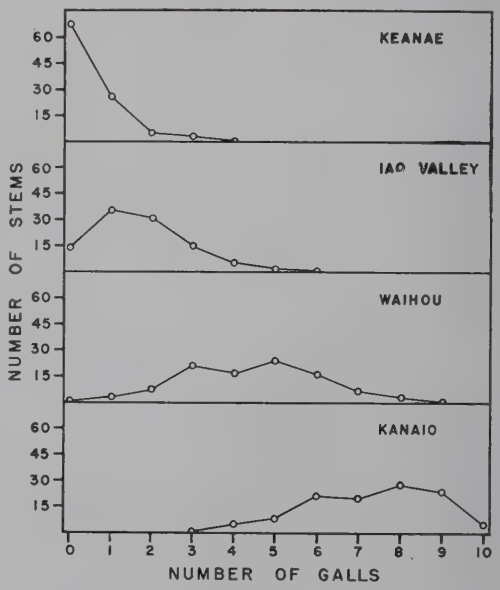

FIG. 3. Graphs showing the intensity of galling in four localities on Maui.

[2] Standard error of mean.

produced, for more individuals are produced per gall where the fly population is high because of the greater number of eggs laid per oviposition site. Another factor is the galling of lateral stems. In all areas a higher percentage of main stems than laterals was galled. However, in heavy infestations where practically 100% of the main stems were galled, most of the laterals were also galled.

Abundance of parasites

The first collections of galls in the fall of 1949 revealed that parasitization was high and that there were 3 principal parasites involved. Subsequently it was found that adult parasites were conspicuously numerous in the pamakani areas in other localities. The gall collections from Maui, Molokai, and Lanai produced many parasites, and the variation in abundance of the 3 principal species in the different localities was pronounced (Table I). At Waihou *B. terryi* was far more

TABLE I. Summary of flies and parasites reared from gall collections made during 1949 to 1957

Locality	Total Number of Collections	Total Number of Adults Emerged				
		Procecidochares utilis	*Bracon terryi*	*Eupelmus cushmani*	*Eurytoma tephritidis*	*Opius tryoni*
MAUI						
Iao Valley	17	2604	751	571	713	0
Kanaio	17	4018	3441	1010	2257	0
Kipahulu	12	1468	105	147	122	1
Waihou						
A	10	5947	2953	58	156	0
B	8	4348	3674	78	193	0
C	5	1347	649	45	141	0
Keanae						
A	13	1377	543	635	367	0
B	10	632	611	439	215	1
North Hana	12	1566	447	213	122	1
Other Localities	17	2678	542	318	1308	0
LANAI	5	1559	551	114	131	0
MOLOKAI	3	322	34	24	123	0
OAHU	20	2036	5	4	359	84
HAWAII	1	176	0	0	0	0

abundant than the other 2 species combined, while at Kipahulu *E. tephritidis* was the predominant species. In other localities on Maui each of the 3 species was responsible for an appreciable part of the total parasitization (Figure 4). Parasitization was appreciably higher in the fall than in the spring (Figure 5). Although the total parasitization varied between seasons, the relative abundance of parasites in respect to each other was in most cases consistent (Figure 6).

DISCUSSION

Although extensive areas of dense pamakani occur on the slopes of Haleakala in the vicinity of Ulupalakua and Kipahulu, Maui, in other localities it occurs more or less as small dense patches in gulches and along steep banks on roadsides on non-agricultural land. Even though the plant density in the plots at Keanae and Iao Valley was similar to that in the plots at Waihou, the over-all abundance of pamakani was considerably higher in the Ulupalakua and Kipahulu areas than elsewhere. In the Ulupalakua area at one time many thousands of acres of valuable grazing land

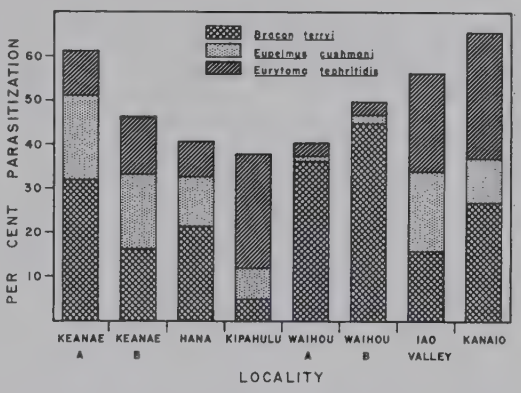

FIG. 4. Graphs showing total parasitization and that caused by each of the three principal parasites at several localities on Maui.

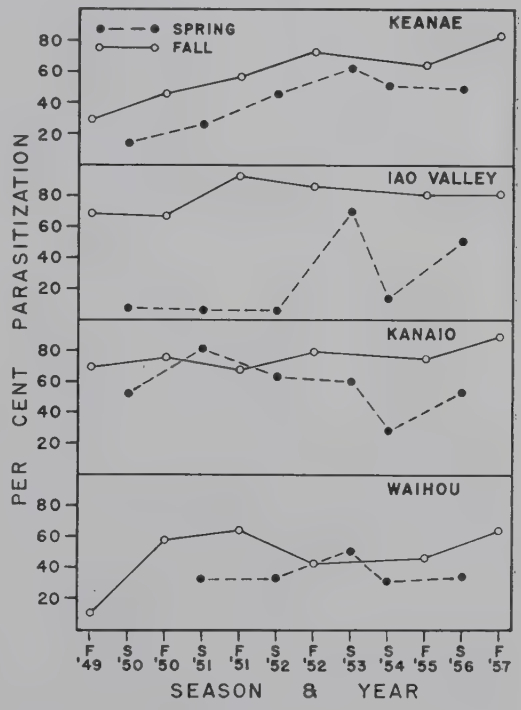

FIG. 5. Graphs showing seasonal and yearly variations in the total parasitization at four of the collection sites on Maui.

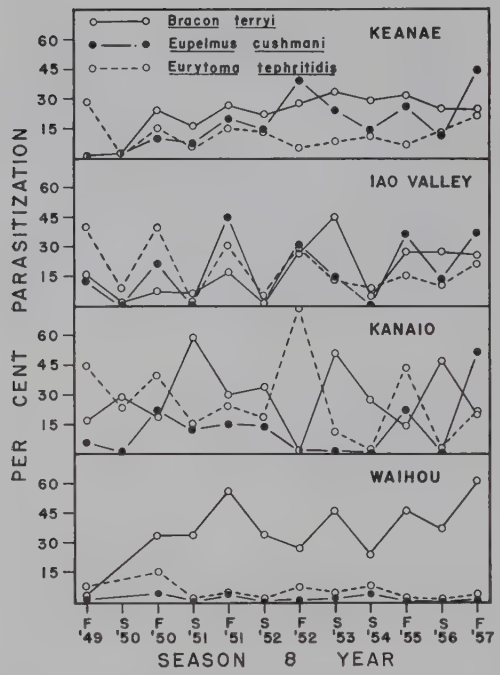

FIG. 6. Graphs showing the fluctuations in parasitization by each of the three principal parasites during different seasons and years.

between 1,000 and 7,000 feet elevation were densely covered with this shrub, which was introduced as an ornamental into that area from Mexico in about 1865.

Immediately following the release of *P. utilis* in the Ulupalakua area in 1945 the fly increased rapidly and became exceedingly abundant in the extensive dense pamakani stands. By 1949 many plants had been killed by the heavy and persistent attack of the fly, and no plants that were free of galls were found in the area. A collection site which was selected in a dense stand at about 4,000 feet elevation at Waihou C in 1949 had to be abandoned in 1952 due to the scarcity of plants, and soon thereafter no plants could be found within a radius of one mile. At the other collection sites, Waihou A and B, located higher up the slope, which were also in dense stands of pamakani in 1949, by 1957 there were so few plants left that widespread search had to be made to obtain adequate samples of galls. Over large acreages in this vicinity the pamakani was gradually thinned out, and the remaining weakened plants became smaller and finally succumbed even in the gulches and on the more northerly steep slopes which appear to be more favorable ecologically to the plant. Thousands of acres of land between 1,000 and 4,000 feet elevation that were once densely covered with pamakani are now completely free of the plant. In many other localities where there were small patches and isolated pamakani plants this weed has been killed in a similar manner. The different stages in the progressive elimination of the weed by the fly can be seen at this time in the Waihou area between 4,000 and 6,000 feet elevation. In other localities with higher rainfall distributed throughout the year the plant grows more or less uninterruptedly, while in localities where there are definite extended dry periods, such as Kanaio, there is little growth except during and immediately following rainy periods. Since the eggs are usually deposited between the young paired leaves before these unfold, the potential number of oviposition or attack points over a period of time is dependent upon the number of stems and the growth rate of the plants. During the rainy season there is flush growth which increases the number of stems available for oviposition. On the other hand, during a dry season there are fewer oviposition sites, and, in addition, continued heavy attack by the fly causes the growing tips to die. Galling affects the normal physiology of the plant as evidenced by shortened stems and reduced foliage production. This may in part explain why the fly has been successful in controlling the weed in certain localities and not in others.

The reduction of pamakani, the only known host or larval food supply of the fly, has no doubt reduced the *P. utilis* population within the general Ulupalakua area. However, the proportion of flies to the remaining available food supply has remained high in the areas where the fly has been effective in the reduction and eventual elimination of the weed. On the other hand, along the Hana coast, where the fly has caused no appreciable reduction in the abundance of the plant, the fly population is low and affects only a small portion of the total food present.

Parasites have been relatively common in all pamakani areas studied, except for the small isolated area on the island of Hawaii. They were especially numerous in the Ulupalakua area if considered on the basis of either parasites per unit area or parasites per pamakani plant, but low on the same bases in the other localities where the fly has not appreciably reduced the abundance of the weed. On the other hand, if the parasite population were to be considered on the basis of available food supply, which is *P. utilis*, the density was high in all localities except the one on Hawaii. Observations on the general abundance of parasite adults in the

field and the information obtained from the samples of galls show that the parasites were more abundant during the fall than in the spring. This seasonal fluctuation was also true of each of the 3 major parasites. Therefore, even though the parasites were dependent upon their host for food, the parasite population was affected more by the other ecological factors than by the population density of their host. The abundance of the different species of parasites in respect to each other also varied with the locality. However, even though the parasitization by *E. cushmani* and *E. tephritidis* at Waihou was low, their actual populations may have been higher than in other localities where the percentages parasitized by them were higher. This is because, as pointed out earlier, in localities like Waihou and Kanaio there are more pamakani plants in the general area, more galls produced per stem and more *P. utilis* produced per gall, than in localities like Keanae. The total parasitization averaged more than 35% in each locality and would be much higher if only the fall collections were considered. From the standpoint of efficiency, the parasites were more or less equally successful, irrespective of the population densities of the fly, in all of these Maui localities studied intensively. Despite the high parasitization, this fly has been able to eliminate pamakani over large acreages above Ulupalakua and Kipahulu, and it appears that the lack of its success in the other localities cannot be attributed to parasitization.

Summary

1. The abundance of a tephritid gall fly, *Procecidochares utilis,* and its role in the biological control of the weed pest pamakani, *Eupatorium adenophorum,* under a wide range of ecological conditions were studied on Maui from 1949 to 1957. In some localities the fly was abundant throughout this period and caused considerable reduction of its host, while in others it was never conspicuously abundant, and had little detrimental effect on the weed.

2. Five species of parasites were reared from the fly. Parasitization was appreciable, often exceeding 50%. A brief resume of the biologies of the parasites and the parasitization caused by each of the 3 major species is presented.

3. The abundance of the fly, of its host, pamakani, and of the 3 major parasites of the fly, are discussed. These are presented graphically and discussed from the standpoint of season and locality.

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SMALL MAMMALS AND OLD FIELD SUCCESSION ON THE PIEDMONT OF NEW JERSEY[1]

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This study of the small mammal fauna in relation to secondary succession on the Piedmont of New Jersey was stimulated by several factors. The first and most important was the careful description of plant succession in this area by Bard (1952) that serves as a basis for the present study. Secondly, many of the fields where Bard

[1] This project was aided by a grant from the Rutgers University Research Council. I am grateful to M. F. Buell, C. Monk and G. K. Reid who read the manuscript and made helpful suggestions.

studied were still available but the need for prompt study was illustrated when one of the fields succumbed to a housing development. Lastly, since these areas are used for field study by ecology classes at Rutgers, it was apparent that precise information was needed on the (1) species of small mammals represented in the seral stages, (2) patterns of mammal distribution relative to vegetational cover in these fields, and (3) the relative mammal population levels in the successional stages.

The seral stages studied were fields whose "age," or elapsed time since last cultivated, was 7, 11, 16, 46 and 66 years. Also, an oak forest formerly known as Mettler's Woods and now referred to as the Hutcheson Memorial Forest served as the climax forest reference stage. The old fields were 1, 5, 10, 40 and 60 years of age at the time that Bard studied them. All of these fields are in Somerset County and are less than 5 miles from Hutcheson Forest near East Millstone, N. J. They have the same general climate, are all located on the Brunswick Shale Formation of the Piedmont physiographic province, and all have soils of the Penn series. Bard made every effort to reduce as far as possible the number of variables affecting community development, but it should be noted that the 66-year field (Bard's 60-year field) apparently was an orchard rather than a cultivated field and should therefore have a somewhat different successional pattern.

Field work was continued from July 8 through August 24, 1956; November 6-7, 1956; February 6-April 10, 1957, and June 13-16, 1957. The field work was done by the author except for the trapping from February through April, 1957 which was done by Mr. Steven V. Kaye. The general procedure was to use 25 Sherman live traps per census period for each plot representing a seral stage. The number of plots trapped per census period varied from 2 to 6. The census period usually lasted 3 days and the traps were checked during the early morning of each day. The traps were spaced at 50 feet intervals in lines 50 feet apart. In the 11, 46, and 66-year fields and in Hutcheson Forest one line of 12 and one of 13 traps were used, while the 7 and 16-year fields were shaped such that two lines of 8 and one line of 9 traps were set. The traps were baited with oatmeal and on several occasions peanut butter was added. Animals were marked by a toe clipping method similar to that used for spadefoot toads by Pearson (1955). The animals were released at the point of their capture after size, pelage, and other characteristics had been recorded. The behavior of the mammals when released and the location of the trap-site was noted in relation to the vegeation cover.

Results

Seral Stages

1. *Seven Year Stage.* This stage was represented by a 4-acre field located on Cedar Grove Lane, 1.6 miles west of Canal Road in Somerset County. It was surrounded by a paved road, by an old orchard, a fence row and a field of approximately the same age, and by a field of about 25-35 years development.

Herbaceous vegetation formed the dominant aspect of the 7-year field and the vegetation could be divided into 2 cover types that served as habitats for small mammals. One cover type that blanketed about half of the area, centrally located in the field, was dominated by goldenrods (*Solidago nemoralis, S. graminifolia*), aster (*Aster ericoides*) and other forbs. The open growth form of this vegetation was such that much light reached the surface of the soil and the layer occupied by small mammals. The second cover type, dominated by broom-sedge (*Andropogon scoparius*), covered about half of the 4 acres and formed the cover on the perimeter of the field. Broom-sedge provided a dense layer of vegetation just above the surface of the soil and light penetration and evaporation through this cover was low. There were many seedlings of woody plants present at this stage and among them were red cedar (*Juniperus virginiana*), bayberry (*Myrica pennsylvanica*), dogwoods (*Cornus florida* and *C. amomum*), smooth sumac (*Rhus glabra*) and others.

This plot was trapped 7 census periods for a total of 622 trap-nights; of these, about half (290) were in goldenrod-aster cover, 307 in broom-sedge cover and 25 trap-nights were in a mixture of these 2 cover types.

The animal most frequently caught in the forb cover was the white-footed mouse (*Peromyscus leucopus*) which was captured 16 times. The short-tailed shrew (*Blarina brevicauda*) was captured twice and the pine mouse (*Pitymys pinetorum*) was taken 4 times. The trapping data in broom-sedge cover were quite different in that there were only 4 *Peromyscus* captured while there were 22 captures of the meadow mouse (*Microtus pennsylvanicus*), 2 captures of *Blarina* and 4 of the masked shrew (*Sorex cinereus*). Three *Peromyscus* and one *Microtus* captures were made in traps of unassigned cover type.

The indication that the 2 cover types in this field supported different faunas was strengthened by the observations of the behavior of mice when

released. The response of released *Peromyscus* could be subdivided as follows: (1) those released in the cover of goldenrod-astors remained in this cover and were usually traced to the openings of an underground burrow system and (2) those released at the boundary of goldenrod-aster and broom-sedge cover reacted positively to the goldenrod-aster cover. All of the *Microtus* were caught in broom-sedge cover and they were never observed to leave this cover when released at the capture point. Rather they would quickly disappear into runways under the mat of broom-sedge cover.

2. *Eleven Year Stage.* This was represented by a field of about 6 acres across the highway from the 7-year field described above. In addition to the highway this field was bordered on the other 3 sides by a field of similar age, and a hedgerow on 2 sides, one of which separated the field from a farm dwelling and out-buildings. At the most, only about one acre, or one-sixth of this plot, was dominated by the goldenrod-aster cover type and, as in the 7-year field, these perennial forbs were in an area of relatively poor drainage. The broom-sedge was denser than in the 7-year stage and there were large areas of essentially unbroken mats of cover. Shrubs and trees such as red cedar, bayberry, 2 species of dogwood, smooth sumac, and others were higher and denser than in the 7-year field.

Of a total of 625 trap-nights recorded in this field, 68 were in goldenrod-aster, 491 were in broom-sedge, 2 were in shrub and 64 were in a mixture of these. From the goldenrod-aster cover only 3 meadow mice were taken while in the broom-sedge cover 33 captures of meadow mice, 10 captures of house mice (*Mus musculus*), 8 captures of short-tailed shrews and 7 of masked shrews were recorded. The only white-footed mouse observed in this field was taken in a large cluster of bayberry shrubs, while 2 captures of house mice were made in mixed cover.

Thus, in this stage there was a great reduction in the white-footed mouse population and an absence of pine mice. The meadow mice, house mice, and short-tailed and masked shrews were the most abundant small mammals and all of these were characteristically taken under the dense ground cover of broom-sedge leaves and stems. In this mat of vegetation runways currently being used were conspicuous and scats, cut grass stems and other signs of activity were obvious.

3. *Sixteen Year Stage.* This stage was represented by a 4-acre plot located on Elizabeth Avenue, 0.3 mile from Amwell Road. This field was bordered by a road, a residence, and, on 2 sides, a hedgerow that marked the boundary between this and other fields. About three-fourths of this field was dominated by broom-sedge cover. There were extensive areas covered by a thick mat of this vegetation, but at the same time in several parts of the field there appeared to be considerable broom-sedge mortality with consequent removal of small mammal cover. The goldenrod-aster cover was less than in previous stages and, together with the shrubs and trees, covered about one-fourth of the field. The woody plants of this stage had considerable areal coverage and provided shelter for small mammals. In addition to the trees mentioned in the previous stages red maple (*Acer rubrum*) was common and a few pin oaks (*Quercus palustris*) were present.

Of the recorded trap-nights for the various types 98 were in goldenrod-asters, 432 were in broom-sedge, 21 in shrub and 46 were in various combinations of these. Twelve white-footed mice were taken in the perennial forbs, 5 were trapped in shrub-tree cover, while 5 *Peromyscus* and 2 meadow mice were taken in mixed cover. Five species were caught in broom-sedge cover; there were 3 captures of *Peromyscus,* 42 captures of *Microtus,* one capture of *Mus,* 5 of *Blarina* and 3 of *Sorex.* It should be noted that in proportion to the amount of trapping effort there was a higher frequency of *Microtus* captures in the broom-sedge of this field than in the 2 earlier stages.

4. *Forty-six Year Stage.* This and the next stage were located on property owned by Mr. Bolmer on Cedar Grove Lane northwest of Middlebush, N. J. The plot of approximately 10 acres was bounded by roads on 2 sides, by the 66-year stage on another, and by the Bolmer residence and gardens on the fourth side. The road borders were excluded from trapping since in these there was more shrub and tree vegetation than normally occurred in the remainder of the field. The cover at this stage was formed by broom-sedge and aggregations of trees and shrubs. While the relative importance of the cover types was not measured, it was obvious that the woody plant cover was greater both in areal extent and in height. However, even with this increase, broom-sedge still occupied extensive areas. This broom-sedge, unlike the same species in the earlier stages, offered poor cover for small mammals as a result of the degeneration of the mat and the widely spaced distribution of the individual plants.

Of the trap-nights recorded for this field 190 were in broom-sedge cover, 139 were in shrub and tree cover, 52 were in mixtures of these, and cover type was not recorded for 111 trap-nights. Since the traps were systematically and uniformly

spaced in the field the number of trap-nights recorded gives a general idea of the extent of coverage by the 2 cover types. The catch in broom-sedge included 8 captures of white-footed mice and one of *Microtus* while under the shrubs and trees only 14 white-footed mice were captured. Four captures of white-footed mice and 2 of short-tailed shrews were made from the traps in cover of mixed type.

The most interesting aspects of the results from this field are (1) the sharp decline of meadow mouse captures and (2) the abundance of white-footed mice in shrub and tree cover. Herbaceous vegetation, primarily broom-sedge, covered extensive areas. One might expect then to find meadow mice abundant, except for the fact that at this stage the dense, homogeneous mat of grass had been broken and instead it was usual to find only isolated plants of *Andropogon* surrounded by larger areas covered by lichens. There was no goldenrod-aster cover and the white-footed mice were trapped more often in clusters of trees and shrubs. Also, it was noted that while the *Peromyscus* might move through areas dominated by broom-sedge they nearly always disappeared underground in the woody plant cover. The behavior of several of these mice upon release in broom-sedge was to run across lichen cover and to avoid the individual broom-sedge plants.

5. *Sixty-six Year Stage.* This stage consisted of an 8-10 acre field located on Cedar Grove Lane as noted above. It apparently represented an abandoned orchard as was indicated by even-spaced aggregations of red cedar corresponding to the original sites of orchard trees. The dead stumps of a few of these trees were found in the center of the red cedar clusters. The shrub and tree cover was quite extensive with only small patches of herbaceous vegetation between them. This relation is illustrated, as above, by the number of trap-nights recorded for cover types. Ninety-six trap-nights were in broom-sedge cover, 227 were in shrub-tree cover, 63 were in a mixture of these and for 240 trap-nights the cover-type was not recorded. One white-footed mouse and 3 short-tailed shrews were taken in the broom-sedge, while 24 *Peromyscus* and 2 *Blarina* captures were recorded for the shrub-tree cover. Twenty-one captures of white-footed mice and 2 captures of short-tailed shrews were made in a mixture of grasses and shrubs. It was quite apparent that the dominant small mammal of this stage was the white-footed mouse and that its capture was associated with shrub and tree cover.

6. *Climax Oak Forest.* A 4-acre section of Hutcheson Memorial Forest, that according to Bard (1952) is the nearest approximation to the local climax oak association, was trapped to provide a frame of reference in the successional picture. The forest has been described by Monk (1957) and was characterized by a shrub cover of *Viburnum acerifolium.* The herbaceous cover in this mature forest was sparse except during the spring when May-apple (*Podophyllum peltatum*) and other herbs flourish. From a total of 499 trap-nights 58 captures of white-footed mice, 8 captures of pine mice and one capture of a short-tailed shrew were made.

Analysis of Cover Types

It has been noted above that vegetation cover composed of goldenrods, asters, and other perennial forbs occupied a large part of the 7-year field and a decreasing amount in the 11 and the 16-year stages. The small mammal data for perennial forb cover combined from these 3 fields are in Table I. The white-footed mouse was the most

TABLE I. A summary of trap-nights, number of captures of each species, and the number of captures per 100 trap-nights according to cover type. Species are listed in order of abundance for each cover type

Broom-sedge 1516 Trap-nights			Goldenrod-Aster 456 Trap-nights		
	No. of Captures	Captures per 100 Trapnights		No. of Captures	Captures per 100 Trapnights
Microtus	98	6.5	Peromyscus	28	6.1
Peromyscus	16	1.1	Pitymys	4	0.9
Blarina	15	1.0	Microtus	3	0.7
Sorex	13	0.9	Blarina	2	0.4
Mus	12	0.8			
All Species	154	10.2	All Species	37	8.1
Shrub and Tree 366 Trap-nights			**Mature Oak Forest 499 Trap-nights**		
Peromyscus	38	10.4	Peromyscus	58	11.6
Blarina	2	0.6	Pitymys	8	1.6
Pitymys	1	0.3	Blarina	1	0.2
All Species	41	11.2	All Species	67	13.4

abundant small mammal in this cover. The aggregate trapping data for the broom-sedge cover type in the 5 fields (7 through 66-year) are given in Table I and it is seen that the meadow mouse was the most abundant small mammal in this type of cover. Trap data for the shrub and trees from the 16, 46, and 66-year fields show the white-footed mouse to be the dominant small mammal with only short-tailed shrews, and pine mice as associates. Similar results were noted in the mature forest.

Two animals, *Peromyscus* and *Blarina,* were trapped in all cover types with the former being the most abundant small mammal in all but the broom-sedge. Two other genera, *Mus* and *Sorex,* were taken only in broom-sedge cover where *Microtus* was the dominant small mammal. *Pityinys* was taken in all but the broom-sedge cover

and was found in the earliest and in the last 2 seral stages. The greatest number of species was taken in broom-sedge. The greatest population density of small mammals was in the mature forest.

Species Account

The masked shrew was observed only in the 11 and 16-year fields. These shrews were limited also to the trapping periods from February through April, 1957. Whether this reflects a seasonal change in abundance or different trapping techniques by the author during the summer and by Mr. Kaye during the winter period is not known; however, in so far as we could determine the trapping techniques were the same.

The short-tailed shrew was caught throughout the year in all stages of succession and in all cover types. A test of the association between the captures of this form and cover type was made by using a 2 × 2 contingency table similar to those of Table II using data from the 7, 11, and 16-year stages. This test showed that although the shrew was caught more often in broom-sedge than in goldenrod cover there was no statistical significance in this association ($\chi^2 = 1.3$). A similar test was made that compared the capture data of *Blarina* for association with broom-sedge or with shrub and tree cover in the 46 and 66-year stage. It failed to give evidence of significant association ($\chi^2 = 2.0$). This apparent lack of association between *Blarina* captures and cover type might be an indication of its vagility which is reflected in its wide distribution throughout the collecting.

TABLE II. An analysis of association between capture data and vegetation cover for data from the 7, 11 and 16 year-fields

Peromyscus leucopus	Catch	No Catch	Total
Broom-sedge	7	1223	1230
Goldenrod	28	428	456
Total	35	1651	1686
	$\chi^2 = 48.0$		

Microtus pennsylvanicus	Catch	No Catch	Total
Broom-sedge	97	1133	1230
Goldenrod	3	453	456
Total	100	1586	1686
	$\chi^2 = 29.9$		

The population of meadow mice increased from the 7 to the 16-year stage as shown in Table III. It has been noted above that this mouse was most abundant in broom-sedge and a test of association between meadow mice and broom-sedge shows a highly significant relationship (Table II). The positive reaction to *Andropogon* or to the runways and nests therein, upon release from traps has been noted previously. It should also be pointed out that it is not the presence of broom-sedge alone but the presence of a heavy mat of broom-sedge cover that seems to be important as shelter for the meadow mice.

TABLE III. Small mammal trapping data for stages in old field succession. The numbers represent the average of the number of different individuals caught per census period per 100 trap-nights

	"AGE" OF PLOT (years)					
	7	11	16	46	66	250+
Total Trap-Nights	622	625	597	492	626	499
Sorex cinereus	0.6	1.3	0.5	...	..	..
Blarina brevicauda	0.6	1.3	1.0	0.4	1.1	0.2
Microtus pennsylvanicus	2.8	3.7	5.5	0.4	...	...
Pitymys pinetorum	0.6	...	...	...	0.3	1.4
Peromyscus leucopus	3.2	0.2	3.3	5.1	5.2	10.0
Mus musculus	0.2	1.6	0.1	...	...	...
Total of All Species	8.2	8.0	10.5	5.8	6.7	11.6

The pine mice were trapped only by Mr. Kaye during the winter season and only in the goldenrod-aster cover of the 7-year stage and in the woody cover of the 66-year field and Hutcheson Forest. Their distribution in relation to cover was very similar to that of white-footed mice in that they apparently showed a negative response to broom-sedge cover and a positive response to the forb and shrub-tree cover.

The captures of the white-footed mouse were strongly associated with perennial forbs in the early fields, and their behavior gave indications of a negative reaction to the broom-sedge (Table II). If data from the 46 and 66-year stages are combined, 9 captures of this species and 277 trap-nights of no capture were recorded in broom-sedge while in the shrub and tree cover there were 38 captures and 328 trap-nights of no capture. Contingency tests of these data show a significant association between captures of *Peromyscus* and shrubs and trees ($\chi^2 = 11.5$). Therefore this species was caught more frequently in perennial forbs in the 7-year stage, in both this and shrub and tree cover in the 16-year stage and then in the latter in subsequent stages.

The house mouse was captured only during the summer seasons and only in a cover of broom-sedge. Of the 12 captures made in this cover, one each was in the 7 and 16-year fields and 10 were in the 11-year field. There is considerable evidence, although not statistically significant, that these mice are associated to a greater degree with *Andropogon* cover ($\chi^2 = 3.6$) than with the goldenrod-aster cover.

DISCUSSION

In some respects the results of this study parallel those of a study in Michigan by Beckwith

(1954). Beckwith found that in the annual-biennial stage the prairie deer mouse (*Peromyscus maniculatus bairdii*) was the most common small mammal although in the perennial grass stage that followed the number of deer mice decreased and the meadow mouse became most common. Data were not obtained on small mammals in the perennial forb stage of goldenrods and asters that followed rather than preceded the grass stage in Michigan. In the shrub and later tree stages the white-footed mouse (*Peromyscus leucopus*) became most common and the meadow mouse population was considerably decreased. Therefore, Beckwith's study revealed that in Michigan, *Peromyscus* is most common in the early and late seral stages while *Microtus* is most abundant in the grass stage. It is especially interesting that in New Jersey *Peromyscus leucopus* fills the *Peromyscus* niche both in the early and late seral stages, while in Michigan *P. maniculatus* fills the niche in the early stages.

The observed relationship between *Microtus* and heavy grass cover has been tested by Eadie (1953) and by Mossman (1955). The former found a significant association between meadow mouse activity and heavy herbaceous cover. Furthermore, Mossman has concluded that there is a significant correlation between the abundance of *Microtus, Sorex, Blarina, Peromyscus* and *Mustela* and light penetration through herbaceous vegetation. Thus, there is good correspondence between these studies and the observations of the present study on the association of *Microtus* captures with a dense homogenous mat of broom-sedge. It would appear from all of these studies that the growth form of vegetation is of first importance in determining small mammal distribution and density.

With regard to interspecies relationships within the seral stages the conclusions of King (1957) from a laboratory study of aggressive behavior in *Mus musculus* and *Peromyscus maniculatus* are interesting. He concluded that the greater aggressiveness displayed by *Mus* would suggest that wherever the 2 met under natural conditions, *Peromyscus* would be driven away by *Mus*. Since *Peromyscus* does not resist the attacks it could easily escape. This type of behavior might explain the near exclusion in the present study of *Peromyscus* from broom-sedge cover where *Mus, Microtus,* and *Sorex* are characteristically found and the fact that the white-footed mouse was most common in all the other cover types where these species were not common. A study of the aggressive relationship between the species represented in this study might well point to causal factors in the observed small mammal-cover associations.

The presence or absence and the relative abundance of small mammals in the various seral stages can be explained on the basis of changes in the types and amount of vegetative cover. For example, the presence of *Sorex, Mus* and *Microtus* in the 7 to 16-year stages is apparently related to the presence of adequate broom-sedge cover. Also, the relative abundance of the mammals is directly proportional to the density and areal extent of this cover type. Likewise the occurrence and density of *Pitymys* and *Peromyscus* are apparently related to the cover of perennial forbs or shrub and tree cover.

The relative abundance of all small mammals may be a reflection of the degree of development of field or grassland aspects from the 7 to the 16-year stages. The grassland aspect degenerated between the 16 and 46-year stages and the small mammal population likewise decreased abruptly in abundance and in species representation. However, the forest aspect began to be prominent with the 16-year stage and continued to increase in extent to the mature oak forest; at the same time the white-footed mouse population apparently also increased as did *Pitymys* in the last two stages. In other words we might think in terms of a grassland and a forest community with a zone of interaction, overlap, or tension occurring temporally somewhere around the 16-year stage. This might even be considered as a temporal ecotone (Pearson 1955) between these two communities. Johnston and Odum (1956) have found essentially similar results in their study of breeding bird populations in relation to plant succession on the Piedmont of Georgia. They conclude from their work and from a review of the literature on bird studies that densities usually increase with increasing ecological age with a leveling off or slight population reduction in the climax stage. However, these authors noted an increase in density of breeding birds through the grassland and grassland-shrubland stages with a decrease in pine forests of 25 and 35 years of age. Then, as an understory of deciduous trees developed, the density of birds increased until there was a slight decrease in the climax oak-hickory forest stage. It is interesting that their results show the same population decrease in the mid-successional period as is shown in this study with small mammals.

Summary

1. A study was made of the relative abundance and species occurrence of small mammals in stages of secondary succession on the Piedmont of New Jersey. The association of trap captures of these

species with dominant vegetation cover types was analyzed.

2. White-footed mice were associated with perennial forbs in the earliest seral stages as well as with shrub-tree cover in the late seral stages. In Michigan, the *Peromyscus* niche of the early seral stages is filled by *P. maniculatus* while *P. leucopus* are found in later stages.

3. As with the white-footed mouse, the pine mouse was associated with perennial forbs in the early stages and with shrub-tree cover in the late seral stages.

4. The captures of meadow mice, masked shrews and house mice were associated with broom-sedge cover of a dense, homogeneous nature that was found in the 7, 11 and 16-year stages, but not in later ones.

5. The relative abundance of the total small mammal fauna increased from the 7 and 11 to the 16-year stage as the field aspect developed, decreased by the 46-year stage and then increased as the forest matured. The species distribution was a reflection of the change from a well developed grassland stage at 16-years to a developing forest aspect afterwards.

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A PHYTOSOCIOLOGICAL ANALYSIS OF THE TALL-GRASS PRAIRIE IN NORTHEASTERN OKLAHOMA[1]

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The tall-grass prairie in northeastern Oklahoma has been described in several reports. Bruner (1931) named this association the Andropogon associes, and described it as a large tongue of prairie extending south from Kansas into northeastern Oklahoma. Blair and Hubbell (1938) designated this same area as the Cherokee Prairie biotic district. The principal plant association was given as the tall-grass sod produced by *Andropogon gerardi,*[2] *Andropogon scoparius, Sorghastrum nutans,* and *Panicum virgatum.* The occurrence of the tall-grass prairie throughout the northeastern part of the state was also shown by Carpenter (1940). A map of the state, showing current vegetative types as related to wild life, has been presented by Duck and Fletcher (1943). The presentation of the tall-grass prairie on this map coincides almost exactly with the northeastern delineations already cited. The only quantitative investigation of the tall-grass prairie in northeastern Oklahoma was conducted by Little (1938), who reported the prairie formation in Muskogee County as the *Andropogon gerardi* association with *Andropogon gerardi* as the dominant but associated with *Andropogon scoparius, Koeleria cristata, Manisuris cylindrica, Panicum virgatum, Paspalum floridanum,* and *Sorghastrum nutans.*

The purpose of this research was to investigate the upland tall-grass prairie in Northeastern Oklahoma and to provide quantitative data relating to the grasses and forbs as they exist in this association.

Location and Description of Study Area

The upland tall-grass prairie was studied as it occurs on three different plots in Rogers County, Oklahoma, approximately 5 miles northeast of Owasso or 15 miles northeast of Tulsa. The area of Plot 1 slopes to the south and east and its cover is continuous, with a minimum of clumping. Plot 2, a gently rolling field of about 60 acres, drains to the northeast. The general cover here is continuous, with some evidence of disturbance

[1] Based on a thesis submitted to the Graduate College of the University of Tulsa, Tulsa, Oklahoma.

[2] Nomenclature of the grasses is according to Hitchcock and Chase (1950); that of the other species follows Fernald (1950).

near the roadside. Plot 3, located 0.3 of a mile to the west diagonally across the road from Plot 2, has numerous mound-like elevations. Sloping to the north, it is continuous with a rather extensive area draining in that general direction.

Climate and Soil

The report of the climatic conditions that prevail during the growing season of the prairie is based upon climatic data which were obtained from the Weather Bureau station at Tulsa, located 12 miles southwest of the study area; also from the station at Heyburn Lake, 40 miles to the southwest; and Grand Lake station 45 miles northeast of the study plots. The solar radiation readings presented as a part of this résumé were recorded at Stillwater, Oklahoma, 75 miles west of the area and were obtained from the Evaporation Data Center at the Weather Bureau in Oklahoma City.

The elevation of the prairie plots studied is approximately 700 feet above sea level. The average date of the last killing frost is March 27. Temperatures of 100°F. or higher are frequently experienced from the latter part of July to early September and are usually accompanied by low relative humidity. The average date of the first killing frost is November 3, making the average growing season 221 days. However, for practical purposes, the growing season of the prairie plots studied terminates in August with the mowing of the plots. The average snowfall for the winter is less than 8 inches. Minimum daily temperatures in January and February occasionally drop to the zero mark but exist for only a day or two.

A graph showing the normal mean temperature, based on a 34-year period, is presented in Figure 1. The yearly mean temperature is 60°F. During the growing season, the average daily maximum temperature is 84°F.; the average daily minimum is 59.2°F. The average monthly temperature is 71.6°F. The record high, occurring in the month of July, was 112°F.; the record low was a — 30°F. in the month of March.

Solar radiation data recorded at the United States Weather Bureau station in Stillwater, Oklahoma, indicate that this area receives an average daily value of direct and diffused solar radiation of 553 Langley[3] during the growing season. The average daily values reach an average maximum of 650 Langley for the month of July with an average minimum of 415 Langley for the month of March (Figure 2). For the period shown on the graph, the greatest amount of solar radiation for any one given hour was 93.6 Langley. Solar radiation is at its maximum during the noon hour on a clear day. Clouds tend to increase the amount of solar radiation in that their lower surfaces reflect and augment direct solar radiation. There is a monthly average of nine clear days during the growing season for the period from sunrise to sunset. Partly cloudy days number twelve, and nine days are cloudy. A preponderance of cloudy and partly cloudy days occurs in the months of March, April, and May.

[3] One Langley = one gr.-cal./cm.^{2}

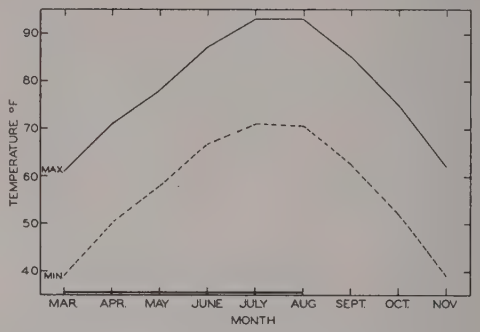

Fig. 1. Graph showing normal mean temperature based on the period 1921-1955. (Here the maximum temperature is represented by a solid black line, while the minimum is a broken line. The normal growing season of the prairie is represented by a continuous bar at the bottom of the lined area. Data obtained from the U. S. Weather Bureau.)

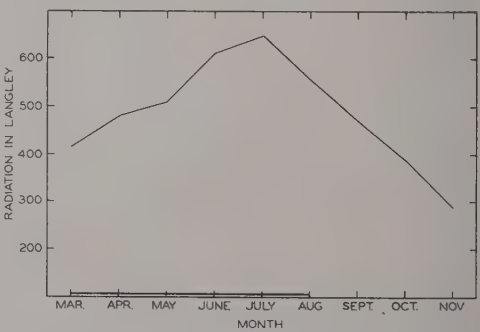

Fig. 2. Graph showing average daily values of solar radiation, direct and diffused, 1955-1956. (Solar radiation reaches its maximum values during the last week in June and the first week in July. The normal growing season of the prairie is represented by a continuous bar at the bottom of the lined area. Data obtained from the U. S. Weather Bureau.)

Rainfall averages approximately 36 inches per year. This precipitation has its greatest concentration in the spring and fall. In the spring an abundance of rain occurs in the form of showers or thunder showers. Average monthly precipitation during the growing season is 3.80 inches. The normal total for a year averages 37.68 inches

(Figure 3). The months of April, May, and June collectively have an average normal total of 4.71 inches. July has a normal total of 2.69 inches. These figures take into consideration traces of sleet, snow and hail.

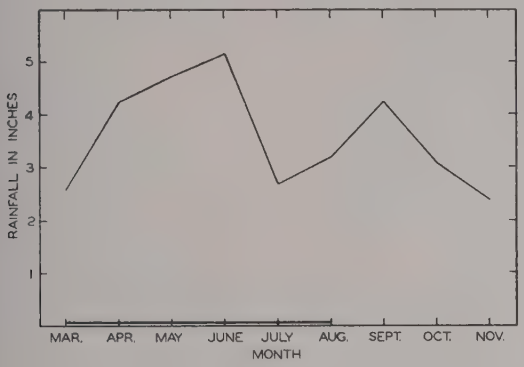

FIG. 3. Graph showing normal mean total precipitation based on the period 1921-1955. (Normally, 45 per cent (16.78 inches) of the yearly normal mean total precipitation occurs during the first 4 months of the growing season. The normal growing season of the prairie is represented by a continuous bar at the bottom of the lined area. Data obtained from the U. S. Weather Bureau.)

A graph showing the mean total evaporation, based on a 13-year period, is presented in Figure 4. The mean total evaporation for the growing season is 61.33 inches of moisture. A maximum of 9.00 inches occurs during the month of July and a minimum of 5.00 inches in March. Evaporation for this area was estimated from readings reported at Heyburn Lake and Grand River Dam stations.

The mean relative humidity of the growing season for the hour 12:30 A.M. has been computed as 75 per cent over a period of 34 years; for 6:30 A.M., 82 per cent; 12:30 P.M., 54 per cent; and at 6:30 P.M., 56 per cent. For a 24-hour period, the mean relative humidity during the growing season is 67 per cent.

Prevailing surface winds are southerly during most of the year. The wind velocity during the growing season has been measured at a mean hourly speed of 11.2 miles per hour; however, winds from the southwest up to 75 miles an hour have been recorded in the month of May.

According to a geologic map of the Tulsa County Area (Oakes 1952), the prairie studied occurs on two different geological formations. Plot 1 occurs on the Oologah Formation, Marmaton group, Des Moines series of the Pennsylvanian System. The Oologah Formation consists of limestone with minor amounts of chert, silt, and shale. Plots 2 and 3 occur on the Seminole Formation, Skiatook group, Missouri series of the

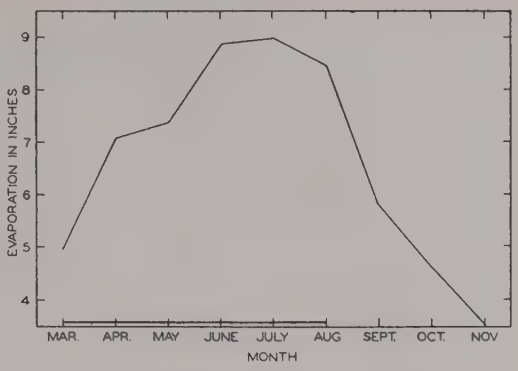

FIG. 4. Graph showing mean total evaporation based on the period 1942-1955. (The data presented in this graph were obtained by using Weather Bureau type Class A Evaporation pans. Circular, 48 inches in diameter, 10 inches deep, operated at ground level. The normal growing season of the prairie is represented by a continuous bar as the bottom of the lined area. Data obtained from the U. S. Weather Bureau.)

Pennsylvanian System. This formation consists of sandstone and shale.

A soil profile made of Plot 1 revealed that the A horizon, a black silt loam of good composition, was 4 inches deep. The B horizon measured 18 inches and was subtended by a C horizon of weathered clay and chert. The C horizon varied in thickness because at intervals it was broken by projections of limestone. In the profile, the C horizon measured 12 inches and covered a solid limestone stratum.

The general area of Plots 2 and 3 revealed a soil profile characterized by an A horizon of rich, black sandy loam 12 inches deep. The B horizon consisting of a sandy clay, was measured to a depth of 24 inches. The C horizon, composed of porous clay and weathered shale, varied in depth but averaged 14 inches in thickness. A more stable sandstone subtended this formation as its D stratum.

The water-retaining capacity of the first six inches of soil was found to be 30.9 per cent in Plot 1, and in Plots 2 and 3, it was measured at 32.3 per cent. The field capacity of the first six inches of soil averaged 25.6 per cent in Plot 1, 22.4 per cent in Plot 2, and 21.9 per cent in Plot 3. The average pH for the first six inches of soil was 6.4 in Plots 1 and 2, and 6.5 in Plot 3.

METHODS

Suitable areas for study were selected after much reconnaissance in a general area northeast of Tulsa. Each plot was selected on the basis of three criteria. First, the general appearance of the vegetation was indicative of little or no disturbance other than the annual mowing. Sec-

ondly, as far as could be ascertained, the areas have not been used for pasture. Lastly, the hay crop is cut only once each year. This cutting is usually done in the month of July. The plots were visited once a week for the purpose of observation and species collection during April and May, then once every two weeks until the study was completed. The actual analysis was accomplished in the last week of July and the first week in August, just prior to mowing.

The vegetation of each area was analyzed by means of a one-tenth square meter quadrat. These quadrats were spaced at intervals of 10 paces along north-south lines situated 30 paces apart and marked at field's edge by stakes. The number of quadrats differ for each area studied: Plot 1, 60; Plot 2, 44; and Plot 3, 30 quadrats. The species in each quadrat were recorded on data sheets along with their living areal cover. Areal cover was estimated to the nearest whole per cent, using, as an aid, metal squares representing 1 per cent and 5 per cent of the total area of the quadrat. Specimen sheets for each species noted on the prairie were filed in the Herbarium of the University of Tulsa. The quadrat data were utilized to compute the average percentages and frequency for each species.

Soil profiles were made at the road cut in each general area, the field capacity of the soil in each plot was determined as recommended by Piper (1944), and the pH, determined from a core of the first six inches of soil, was obtained for each area. A Beckman pH meter, Model H2, was used in measuring the hydrogen-ion concentration of the soil samples. Climatic data were not taken from the study area because of the fortunate proximity of the United States Weather Bureau station, which is situated twelve miles from this area.

Results

An analysis of prairie Plot 1, prepared from the statistics of 60 quadrats and expressed in terms of average areal and frequency percentages, is presented in Table I. Here, sixteen species of an average areal cover of 0.5 of one per cent or greater were represented within the quadrats. The dominant species are the two grasses *Andropogon scoparius* and *Andropogon gerardi*. Significant species are *Panicum scribnerianum, Solidago missouriensis* var. *fasciculata, Sorghastrum nutans, Aristida oligantha, Sporobolus asper,* and *Panicum virgatum*. The average areal cover for all species encountered in the quadrats is 52.4 per cent.

In Plot 2, the analysis of 44 quadrats revealed

Table I. Average areal cover (with standard errors) and frequency percentages of principal species in Plot 1

Species	Areal cover (%)	Frequency (%)
Andropogon scoparius	14.0 ± 1.0	100
Andropogon gerardi	7.0 ± 1.2	73
Panicum scribnerianum	4.2 ± 0.6	73
Solidago missouriensis var. *fasciculata*	3.3 ± 0.8	33
Sorghastrum nutans	2.7 ± 0.4	72
Aristida oligantha	2.4 ± 0.4	50
Panicum virgatum	2.2 ± 0.8	30
Sporobolus asper	2.0 ± 0.5	40
Solidago missouriensis var. *missouriensis*	1.9 ± 0.5	18
Eryngium yuccifolium	1.9 ± 1.0	7
Silphium laciniatum	1.4 ± 1.4	2
Aster patens var. *gracilis*	1.3 ± 0.3	30
Aster ericoides	1.0 ± 0.4	15
Carex sp.	1.0 ± 0.2	68
Coreopsis grandiflora	0.8 ± 0.2	8
Sporobolus sp.	0.5 ± 0.2	8
All species encountered	52.4	

that, of 17 species greater than 0.5 of one per cent, the dominant species were *Andropogon gerardi* and *Andropogon scoparius* (Table II). Important associated species consisted of *Panicum virgatum, Panicum scribnerianum, Aristida oligantha,* and *Sorghastrum nutans*. All species encountered in this plot constitute an average total cover of 49 per cent.

Table II. Average areal cover (with standard errors) and frequency percentages of principal species in Plot 2

Species	Areal cover (%)	Frequency (%)
Andropogon gerardi	7.1 ± 4.2	89
Andropogon scoparius	7.5 ± 1.4	86
Panicum virgatum	4.8 ± 1.0	59
Panicum scribnerianum	4.2 ± 0.6	82
Aristida oligantha	2.7 ± 0.5	59
Sporobolus asper	2.7 ± 0.8	34
Sorghastrum nutans	2.5 ± 0.5	77
Aristida purpurascens	2.0 ± 0.7	30
Solidago missouriensis var. *missouriensis*	2.0 ± 0.6	25
Aster patens var. *gracilis*	1.1 ± 0.4	23
Manisuris cylindrica	0.9 ± 0.4	15
Liatris aspera	0.6 ± 0.5	5
Bouteloua hirsuta	0.6 ± 0.4	9
Leptoloma cognatum	0.6 ± 0.3	11
Hieracium longipilum	0.5 ± 0.2	14
Carex sp.	0.5 ± 0.1	77
Coreopsis grandiflora	0.5 ± 0.2	30
All species encountered	49.0	

The results of an analysis of 30 quadrats in Plot 3 indicate that *Andropogon gerardi* is most certainly the dominant species with *Andropogon scoparius* a likely associated dominant (Table III). In this study area, only 12 species exceed 0.5 of one per cent with an average total cover of

51.6 per cent. Important associated species are *Aristida oligantha, Panicum virgatum, Manisuris cylindrica,* and *Sorghastrum nutans.*

TABLE III. Average areal cover (with standard errors) and frequency percentages of principal species in Plot 3

Species	Areal cover (%)	Frequency (%)
Andropogon gerardi	21.1 ± 2.9	97
Andropogon scoparius	8.8 ± 1.9	90
Aristida oligantha	5.2 ± 1.0	77
Panicum virgatum	4.1 ± 0.9	70
Manisuris cylindrica	2.9 ± 0.6	63
Sorghastrum nutans	1.3 ± 0.6	53
Koeleria cristata	1.0 ± 0.4	27
Sporobolus asper	1.0 ± 0.6	23
Helianthus mollis	1.0 ± 0.3	23
Panicum malacophyllum	0.9 ± 0.4	23
Chloris verticillata	0.7 ± 0.6	7
Panicum scribnerianum	0.5 ± 0.2	23
All species encountered	51.6	

DISCUSSION

In this investigation, any species evidencing an average frequency of 50 per cent or greater, and at the same time possessing a more significant areal cover in relationship to all other species represented, has been designated as a dominant species. Areal cover was used in making the analysis for two reasons. First, according to Bauer (1943), areal cover gives the best relationship between various species, an opinion accepted as evidenced by the use of areal cover in the works of Oklahoma grassland ecologists (Smith, 1940, Penfound, 1948, Rice, 1952, and Kelting, 1954); the second reason, stemming from the first, is that the use of this common denominator would allow for a more valid comparison of the results with the findings of these investigators. A one-tenth square meter quadrat was used in analysis because, as shown by Kelting (1954), quadrats of this size produced close agreement between frequency and areal cover in determining quantitative relationships between species.

The analysis of the three tall-grass prairie plots revealed that *Andropogon gerardi* and *Andropogon scoparius* are co-dominant species. The important associated grasses, presented in decreasing order, are *Panicum virgatum, Panicum scribnerianum, Aristida oligantha, Sorghastrum nutans, Sporobolus asper, Manisuris cylindrica, Koeleria cristata,* and *Aristida purpurascens.*

The important forbs were *Solidago missouriensis* var. *missouriensis, Aster patens, Helianthus mollis, Aster ericoides, Silphium laciniatum,* and *Coreopsis grandiflora.* While the species representation of forbs far exceeds the grasses in number, in Plot 1, 27 species of forbs constitute 13.4 per cent of the average total cover, in Plot 2, 14 species provide an areal cover of 6.4 per cent, and in Plot 3, 10 species produce only 3.7 per cent. The sedges, lacking significant areal cover, are present in more than 75 per cent of all the quadrats.

A comparison of Plots 1, 2, and 3 reveals several interesting relationships (Table IV). Except for a few instances, when a species is represented in Plots 1 and 2 its areal cover and frequency are very similar. The same degree of evident similarity is lacking when the species of Plot 2 are contrasted with the species of Plot 3, even though these plots are only one hundred yards apart.

TABLE IV. Comparison of average areal cover and frequency percentages of principal species in Plots 1, 2, 3

Species	Areal Cover (%)			Frequency (%)		
	Plot			Plot		
	1	2	3	1	2	3
Andropogon gerardi	7.0	7.1	21.1	73	89	97
Andropogon scoparius	14.0	7.5	8.8	100	98	90
Aristida oligantha	2.4	2.7	5.2	50	59	77
Aristida purpurascens		2.0			30	
Aster ericoides	1.0			15		
Aster patens var. *gracilis*	1.3	1.1		30	23	
Bouteloua hirsuta		0.6			9	
Carex sp.	1.0	0.5		68	77	
Chloris verticillata			0.7			7
Coreopsis grandiflora	0.8	0.5		8	30	
Eryngium yuccifolium	1.9			7		
Helianthus mollis			1.0			23
Hieracium longipilum		0.5			14	
Koeleria cristata			1.0			27
Leptoloma cognatum		0.6			11	
Liatris aspera		0.6			5	
Manisuris cylindrica		0.9	2.9		15	63
Panicum malacophyllum			0.9			23
Panicum scribnerianum	4.2	4.2	0.5	73	82	23
Panicum virgatum	2.2	4.8	4.1	30	59	70
Silphium laciniatum	1.4			2		
Solidago missouriensis var. *fasciculata*	3.3			33		
Solidago missouriensis var. *missouriensis*	1.9	2.0		18	25	
Sorghastrum nutans	2.7	2.5	1.3	72	77	53
Sporobolus asper	2.0	2.7	1.0	40	34	23

While not contained in Table IV, an examination of the data sheets reveals a similar situation for species with an areal cover of less than 0.05 per cent.

In Plot 3, where 21 per cent of the cover is *Andropogon gerardi,* the only species (with the exception of *Helianthus mollis*) above the 0.05 per cent level are the grasses. First it was thought that the disappearance of the forbs in the quadrats was due to an inadequate number of quadrats taken in the analysis. However, an examination of the species-area curve on the original field data sheet lend credibility to the fact that sampling was adequate. Even a casual observation revealed that only a few forbs were visible in the plot. Possibly the increased root content of the sod produced by the amount of *Andropogon gerardi*

acts to exclude or reduce not only the cover of the forbs, but also their distribution in this community. The areal cover and frequency for most species in Plot 3 exceeds that of the same species in Plot 2. The co-dominants in Plot 3 possessed an areal cover approximately 7.8 per cent greater than Plot 2 with an average frequency increase of 6 per cent. Further investigation will be necessary before any valid conclusions can be formulated in regard to the variation exhibited in Plot 3.

The climatic factors are relatively constant for all three prairie plots because of their proximity to each other and the similarity of topography for each plot. The growing season of the year 1955, in which this investigation was conducted, was preceded by a period of below average precipitation. The year 1955 fell short of the normal precipitation values by 8.7 inches. After the mowing was completed, the owner of Plot 1 estimated the loss of hay yield due to the dry growing season at 50 per cent. It would seem reasonable that the areal cover would be somewhat reduced by a dry growing season, however, not to the extent of the total estimated reduction of hay crop.

Edaphic factors, however, could contribute some variability. The soil in Plot 1 evidences a thinner A horizon than Plot 2 and Plot 3. The structure of the A and B horizon of Plot 1 is a silt loam while Plots 2 and 3 have a sandy texture. Also, the field capacity of Plot 1 is slightly greater than Plots 2 and 3. The pH is constant at 6.4 for Plots 1 and 2, with a slight variation of 0.1 (6.5) for Plot 3.

The findings of this investigation are generally in agreement with the reports of other workers who have described the tall-grass prairie. This might be expected because the prairie, as a closed community, keeps out species that are not native to it and when not seriously disturbed, perpetuates constant characteristic species.

Of the species listed by Bruner (1931), the Andropogons occurred in all three areas, while *Sorghastrum nutans,* occupying an important role in the grassland in this association, was found as one of the lesser grasses in all three areas. The species *Elymus canadensis, Elymus virginicus, Elymus striatus,* and *Spartina michauxiana* were not encountered in any of the quadrats, nor were they collected as a result of reconnaissance in the prairie plots. There is much agreement with the findings of Little (1938), who studied the tall-grass prairie in Muskogee County in northeastern Oklahoma. Only one species considered by Little as significant, *Paspalum floridanum,* was not encountered in quadrats but was collected in the prairie plots. Blair and Hubbell (1938) reported as characteristic species on the limestone soil *Bouteloua curtipendula, Buchloe dactyloides,* and *Andropogon saccharoides.* In Plot 1, which occurs on the limestone formation, only *Bouteloua curtipendula* was of significant occurrence. The other two species were neither counted in the quadrats nor collected from the plot. Other species reported in this work were found to occur in the quadrats.

Summary

The upland tall-grass prairie as it occurs in northeastern Oklahoma was studied in Rogers County approximately 15 miles northeast of Tulsa. This investigation was conducted during the growing season of the year 1955, and the actual analysis was accomplished during the last week of July and the first week in August of that same year. The areas studied occur on two different geological formations—Plot 1 on the Oologah Formation and Plots 2 and 3 on the Seminole Formation.

The dominant species were *Andropogon gerardi* and *Andropogon scoparius,* with *Panicum virgatum, Panicum scribnerianum, Aristida oligantha, Sorghastrum nutans, Sporobolus asper, Manisuris cylindrica, Koeleria cristata,* and *Aristida purpurascens* as the associated grasses. The important forbs were *Solidago missouriensis* var. *missouriensis, Helianthus mollis, Aster ericoides, Silphium lacinatum,* and *Coreopsis grandiflora.*

There appears to be no significant difference in the average areal cover and frequency of species as they occur on the Oologah and the Seminole Formations. Sufficient evidence is lacking to explain the variations that do exist in a comparison of Plot 2 with Plot 3, and further investigation will be required before any valid conclusions can be reached.

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THE RELATION OF RADIAL GROWTH TO MAXIMUM AND MINIMUM TEMPERATURES IN THREE TREE SPECIES

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One of the objectives of physiological ecology is to study and express the relationships of the various plant processes to their individual controlling factors. Daily measurements of tree growth made with the Fritts dendrograph (Fritts and Fritts 1955) were demonstrated to be highly correlated with environmental factors and to lend themselves to a multiple regression analysis (Fritts 1958). By means of the resulting equation it was possible to represent the effects of changes in one factor upon daily growth while all other independent factors considered in the regression were held mathematically constant.

Methods

During the growing season of 1957 daily radial growth was measured in two white oaks (*Quercus alba* L.) and one sugar maple (*Acer saccharum* Marsh) in an oak-hickory ravine forest near Charleston, Illinois. The trees are on a 20-30° SSE-facing slope about 150 feet from stream bed to top. White oak No. 1, 22.2 inches dbh, is located 76 feet from the top of the slope, and is surrounded by somewhat younger trees which appear to be secondary growth. White oak No. 2, 21.2 inches dbh, and the sugar maple, 18.2 inches dbh, are near the bottom of the slope approximately 40 feet up-slope from the stream bed. They are at about the same elevation and are separated by a distance of about 29 feet. Both are surrounded by trees of approximately the same size as the study trees.

The daily growth (beginning at 6 am CDT) of each tree was punched on IBM cards along with daily maximum and minimum temperature, daily rainfall, solar radiation, solar radiation of 1, 2, 3, 4, and 5 days previous to growth, vapor pressure deficit, and time in number of days from the beginning of the growing season (April 14-August 31). Temperature and rainfall data were measured at the official Charleston weather station, located 2 miles north of the study area. Dewpoint data for calculating the vapor pressure deficit were obtained from the Coles County airport, 7 miles west, and solar radiation data from the pyrheliometer at the University of Illinois, 45 miles north. On-the-spot measurements are now being made, but were not obtainable in 1957 because of lack of equipment and manpower. However, in the relatively level terrain of Illinois, day-to-day regimes for temperature, solar radiation, and humidity at nearby stations are correlated, and even though less reliable than local measurements, can give meaningful results in a correlation analysis.

The measurements made during 1958 substantiate this correlation. Solar radiation measurements at Urbana exhibited a correlation of .705 with equivalent measurements made in Charleston during July and August, 1958. Rainfall measurements at the Charleston weather station and temperature measurements at Charleston and at the airport did not deviate greatly from those made in an open field adjacent to the study area.

Analysis and Results

A multiple curvilinear regression analysis with 17 variables was run on daily observations for the

140-day period by the statistical service at the University of Illinois. The variables were: daily growth, maximum temperature, the square of maximum temperature, minimum temperature, the square of minimum temperature, rain, the square of rain, solar radiation, solar radiation of the previous day, solar radiation 2 days previous, solar radiation 3 days previous, solar radiation 4 days previous, solar radiation 5 days previous, vapor pressure deficit, the number of days from the beginning of the growing season, the square of the same, and the cube of the same. The analysis would probably have been improved and a higher index of multiple correlation obtained if the square of daily solar radiation and the square of vapor pressure deficit could have been included, and also if more on-the-spot environmental measurements, including soil moisture, could have been made (Fritts 1958).

However, rainfall during the growing season was high and temperatures were not extreme, so low soil moisture was probably not a limiting factor until near the end of the measured period. With the rain from the hurricane in late June, monthly precipitation from May-August averaged 2.11 inches above normal and the temperatures averaged slightly below normal.

The partial regression coefficients for growth on minimum temperature (Table I) are negligible, and when compared with their standard error, none differed significantly from 0. However, the coefficients for growth of the white oaks on maximum temperature and the square of maximum temperature are significantly different from 0 at the 5% level. The corresponding coefficients for sugar maple, though high, are not significant when considered separately. However, by using the coefficients of both maximum temperature and maximum temperature squared to plot a curve with its .95 confidence band (Fig.1), the relationship has a less than 5% chance of fitting a horizontal line and being 0 (Ezekiel 1941).

Other partial regression coefficients, when compared with their standard errors, are also significantly different from 0 at the 5% level. For white oak No. 1, the coefficient for growth on number of days is significant; for white oak No. 2, the coefficients for growth on solar radiation of the previous day, number of days, the same squared, and the same cubed are significant; and for the sugar maple, growth on rain, rain squared, solar radiation of the measurement day, solar radiation of 5 days previous, vapor pressure deficit, number of days, the same squared, and the same cubed are all significant.

The partial regression coefficients for temperature, however, are probably more valid than the coefficients for the factors named above. Fritts (1958) demonstrated that radial growth of beech during 1954-1955 was controlled more by temperature and soil moisture than by other environmental factors. These two factors were of comparable magnitude in their effects on radial growth. But during 1957, the higher rainfall maintained abundant soil moisture, and on the well drained slope where the oaks and sugar maple are located, variations in moisture should not have been as limiting. What effects soil moisture did have on growth would be associated with, and therefore statistically parceled out to, factors other than temperature—mainly vapor pressure deficit and rainfall.

TABLE I. Partial regression coefficients and their standard errors for daily radial growth on maximum and minimum temperatures, adjusted index of multiple correlation, and adjusted standard error of estimate. Growth is in thousandths of inches and temperature in degrees Fahrenheit/100. All 16 independent variables, including temperature, were used in computing the adjusted index of multiple correlation and the adjusted standard error of estimate. The partial regression coefficients represent the relation of growth to temperature after the effects of the other variables have been removed

	White Oak No. 1	White Oak No. 2	Sugar Maple
Maximum temperature	+1.721±0.790*	+3.059±1.135*	+0.997±0.856
(Maximum temperature)²	−0.895±0.515*	−1.791±0.740*	−0.757±0.558
Minimum temperature	+0.092±0.522	+0.022±0.750	+0.038±0.566
(Mimimum temperature)²	−0.012±0.460	+0.175±0.661	+0.103±0.498
Adjusted index of multiple correlation	+.714**	+.649**	+.820**
Adjusted standard error of estimate	0.040	0.058	0.044

*Significant at the 5% level.
**Significant at the 0.5 % level.

The relations between maximum temperature and daily radial growth of white oak No. 2 and the sugar maple, as defined by the coefficients in Table I, are plotted in Figure 1 with their .95 confidence bands (Snedecor 1956). It appears as if the shapes of the two curves in relation to the point of optimum growth are significantly different at the 5% level. The most probable maximum temperature for optimum growth in the white oak No. 2 is 85°F. while in the sugar maple it is 66°. The growth rate of the white oak varied directly with temperature from a maximum of 50-85°, with an apparent increase in rate of 2.24 thousandths of an inch per day over this range. The growth rate began to decline with higher temperatures. The growth rate of the sugar maple increased by 0.19 thousandths of an inch per day between 50-66° and then decreased by 0.64 thousandths between 66-95°.

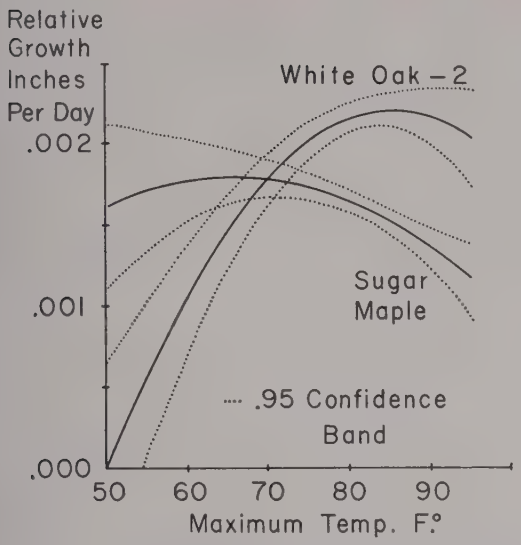

FIG. 1. The relation of daily radial growth of white oak No. 2 and the sugar maple to maximum temperature with the approximate .95 confidence bands, within which the true curves lie.

As is indicated by the wider confidence band in the lower temperature range, the relationships here have the lowest probability of being accurately determined in this particular analysis. In addition, since only 4 days out of the total of 140 had maximum temperatures lower than 60°, any divergent trend at these lower temperatures would have relatively little effect upon the general shape of the fitted curve. Subsequent graphical multiple regression analyses (Ezekiel 1941) were made of the daily radial growth (in the same two trees) on temperature, soil moisture, and time for the period April 11 through May 5, 1958, when low temperatures were common and high temperatures infrequent. The resulting growth curves over this lower temperature range indicate that there is little growth with daily average temperatures of 45° or below, but as the average temperature increases in the 45-60° range, the growth rates in both trees increase. But the difference between the maximum and average temperature of each day was also included as another variable in the analyses, and only the growth of sugar maple shows a significant relationship represented by a decline in growth rate as this difference increases.

These graphical analyses indicate that if in the present study there had been more days of low maximum temperatures and a third degree polynomial had been fitted to these data to allow for a second inflection, the curves would be altered in the 50-60° range. They would probably be more nearly horizontal around maximum temperatures of 50°F. and would turn upward between 50 and 60°, but from 60 to 95°, the curves would probably not differ significantly from those in Figure 1.

The third tree, white oak No. 1, which was upslope from the other two trees, had a lower growth rate than white oak No. 2, but the curve of growth on maximum temperature (Fig. 2) is approximately the same, with an optimum at a somewhat higher temperature (96°F.).

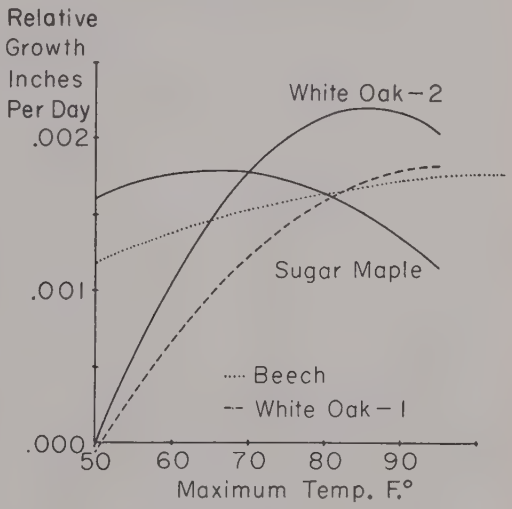

FIG. 2. The relation of daily radial growth of the two white oaks, the sugar maple, and beech to maximum temperature.

DISCUSSION

From the data presented it is apparent that radial growth in the white oaks and the sugar maple is influenced more by the maximum than the minimum temperatures and that the two species are affected differently by changes in the maximum temperature. High maximum temperatures appear more limiting to radial growth of the sugar maple while low maximum temperatures appear more limiting to radial growth of the white oaks.

In Figure 2 the curves of growth on maximum temperature for the three trees are presented along with a similar curve for maximum temperature and daily growth of beech (*Fagus grandifolia* Ehrh.) (Fritts 1958). This curve represents the average radial growth of six beech trees located near Columbus, Ohio, during the growing seasons of 1954 and 1955. From these curves it is apparent that the growth-maximum temperature relationship for the six beech trees more closely approximates the curve for the white oaks than

that of the sugar maple. However, the optimum growth rate in beech occurs at maximum temperatures a little above 100°F., a somewhat higher optimum temperature than for white oak. At lower maximum temperatures, the growth rate of beech appears less reduced than the growth rate of white oak.

These differences between species as represented in Figure 2 appear to be greater than the differences between individual trees of the same species. The daily growth of six beech trees (Fritts 1956) and their individual regression equations appear to be generally similar even for trees in unlike environments. For example, in all six trees and during both years, the optimum maximum temperature for growth was never below 100°F. The greatest differences that do occur are in the relative statistical significance of the individual coefficients and cause only slight differences between the relative shapes of the curves. The same appears to be true in the case of white oak. The growth patterns of the two white oaks are similar even though these trees are in unlike environments. But the sugar maple and white oak No. 2, even though in similar environments, exhibit distinctly different equations and growth patterns.

How do these growth-temperature curves relate to the ecological and geographical ranges of these three species? Braun (1950) discusses the distribution of these species in her treatment of the deciduous forest, and Minckler (1957) and Godman (1957) discuss the silvical characteristics of white oak and sugar maple, respectively. In Illinois, white oak is most abundant on the south- and west-facing slopes, where maximum temperatures are high, while sugar maple is more restricted to the ravines and north-facing slopes. Beech does not extend into central Illinois, but we can compare its north-south range to those of the other two species. Sugar maple occurs farthest north, then beech, and then white oak. Beech and white oak both occur as far south as southern Georgia and northern Florida, while sugar maple "is not found in the south Atlantic or Gulf Coastal Plains," but does extend into the hills of east Texas and Louisiana (Godman 1958). On the coastal plains beech and white oak are dominants in the mesophytic mixed hardwoods communities of ravine slopes (Braun 1950). Beech and white oak both reach their best development in the western Appalachian Mountains and Ohio Valley, while sugar maple reaches its best development in the lake states, or farther south on north-facing slopes and at higher elevations in the Appalachian Plateau.

The curves in Figure 2 suggest a possible physiological basis for the distribution of these species. The high temperatures of the southeast would be much more limiting to radial growth of sugar maple than to that of white oak and beech, while the greater frequency of low maximum temperatures to the north would be most limiting to white oak and least limiting to sugar maple. On the basis of this fact, one would expect sugar maple to have the most rapid radial growth in cooler climates; or, further south, in the microclimates of north-facing slopes, in ravines, or at higher elevations. Beech and white oak would have their optimum rates of radial growth in more southerly regions, or in microclimates where temperatures may commonly reach higher maxima.

The inferring of such causal relationships on the basis of just a few measured trees is not conclusive. Genetic variability over the range of a given species as demonstrated in sugar maple by Kriebel (1957) does exist, and this may contribute to physiological as well as structural differences. However, the data presented here suggest a possible explanation for the local distribution and geographical limits of the three species, which will be verified or disproven only by more extensive measurements during subsequent years and in different localities.

The writer wishes to thank Dr. K. E. Damann and Dr. A. W. Brown for the use of the study area, and Mr. Richard Phipps for his responsibility in maintaining the instruments through the summer months. The writer is also indebted to the Statistical Service of the University of Illinois for the computations in the regression analyses. The study was partially supported by a grant from the Illinois State Academy of Science and by the Department of Botany, Eastern Illinois University.

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A STUDY OF THE ROOT SYSTEMS OF CERTAIN SAND DUNE PLANTS IN NEW MEXICO[1]

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Arid and semi-arid regions are very favorable areas in which to study the rooting habits of plants. This is partly because the environmental features are severe, so that the responses on the part of the plants are correspondingly effective for survival and partly because the sparse distribution of the plants permits ready erosion of the soil by wind and water to permit access to the wide-spread and deeply penetrating root systems.

The dual functions of roots in providing anchorage and absorptive organs is well represented in xerophytic plants by the differentiation of the root system, in its later stages, into separate anchoring and absorptive organs or both. Cannon (1911) observed the root systems of different perennials growing in the vicinity of the Desert Laboratory, Arizona, and noted that they were "extremely variable as regards depth of penetration, lateral extent, and other characteristics, and that no one type of root can be said to be the prevalent one." Similarly Helmers *et al.* (1955) reported marked differences in "depth of penetration, lateral spread, number, and size of main and branch roots," for different species of chaparral plants in southern California. Woods (1957) attributed the shallow root systems of several woody species growing on the sand hills of the southeastern Coastal Plain as due to a combination of light rainfall, low fertility, and higher temperatures in the upper few inches of soil.

The present paper includes descriptions of a number of plants inhabiting the sand dunes of a section in north central New Mexico. The dunes extend for about 20 miles along an intermittent stream which carries considerable water in spring from melting mountain snow but during the rest of the year it has very little or no surface water flowing through it. The dune area most intensively studied is about one mile away from the river and is characterized by abundantly shifting sand over a considerable area. Most of the work was done on the dunes in the vicinity of the Santa Ana and Zia Indian Pueblos. The elevation is about 6000 feet and in the more stable soil around the dune area one-seeded juniper, *Juniperus monosperma* (Engelm.) Sarg. is the most prominent plant. In the shifting sands (Fig. 1) *Ipomoea leptophylla* Torr., *Dalea scoparia* A. Gray, and *Chrysothamnus nauseosus* (Pall.) Britton are the most conspicuous large plants.

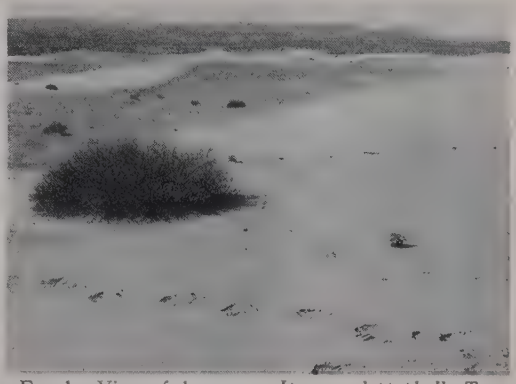

FIG. 1. View of dune area, *Ipomoea leptophylla* Torr. in left foreground.

In some places the sand has been blown off to expose a hardpan of caliche but for the most part the sand is formed in dunes many feet thick. In one exposed area, over 12 feet in depth, the soil was made up of the following strata from top to bottom:

(1) 3′ 6″ loose sand, upper layer
(2) 2′ 6″ sandy clay
(3) 1′ 2″ washed river gravel
(4) 1′ 6″ hard packed clay (caliche)
(5) 4′ 2″ coarse gravel
(6) another gravel layer, thickness not ascertained.

The loose sand is finely uniform, of high silicon quality, and is used commercially in preparation

[1] This research was supported by a grant from the National Science Foundation.

of plaster; in many areas it is over 10 feet thick depending on the amount of shifting of the sand. Moisture was present in the upper sand layers to within about 6 inches of the surface; the clay hardpan was quite dry, but the gravel layer about nine feet beneath the surface had considerable moisture.

All drawings in the paper were made by Serafin Ramon, who assisted in the study.

Methods

Root systems of 13 species were examined from several sites extending along a 10 mile stretch of dunes. At least 4 plants of each species were removed for study. The roots of large plants were exposed by digging trenches beside them and following out lateral roots near the surface wherever possible. Small plants were removed completely and the entire root system preserved in jars of F.A.A. These roots and at least one specimen of the top of each species are in the herbarium at the University of New Mexico. Where large plants could be found growing near an arroyo or stream bank the soil was cut back to expose the root system.

Observations include: depth of penetration, amount of lateral growth, areas of greatest concentration of roots; distinguishing characteristics, such as type of branching; mycorrhizal relationships, color of roots, and relationship to any other plants in the vicinity.

Measurements were made of the length and diameters of the roots by means of calipers and tape measure and the small roots were examined with a compound microscope for root hairs and mycorrhiza. Measurements on the small roots and root hairs were made by means of an ocular micrometer according to the method previously described (Dittmer 1937).

Results

Plants with Tap Roots

1. *Ipomoea leptophylla* Torr. is the most conspicuous of the larger species on the dunes and throughout most of the area. The large specimens are about 2 feet tall and have a diameter spread of 5 or 6 feet. In July very showy reddish lavender tubular flowers are produced over much of the plant. In September, long before frost, the plant turns brown and by late October most of the tops have been blown away. This species has the morphological characteristics in its root one might expect, but seldom finds, in plants native to arid and semi-arid regions. The root forms a large tap (Fig. 2) which becomes rather bulbous about two feet or more beneath the surface. In most of the plants of this species examined the tap root grew straight down to a depth of six feet, then forked and trailed off laterally quite some distance. A few laterals branched off higher along the tap root but they were small in diameter and not very long.

Fig. 2. Large tap root of *Ipomoea leptophylla* Torr. The large lateral to the left was pulled upward to get it out of the way and into the picture.

The largest plant of this species examined had a tap root, which when removed from the soil, weighed 49 lbs. and 4 oz. The total length of this tap root was 129.5 cm; its maximum diameter was 26.6 cm; and it had 17 laterals arising from it. The longest lateral removed intact was 334.8 cm with a basal diameter of 2.9 cm. The largest of the other laterals had a basal diameter of 4.8 cm and the smallest had a basal diameter of 0.6 cm.

This tap root is a large water storage reservoir. At the end of one week its total weight had dropped to 40 lbs. 2 oz. and at the end of 65 days it weighed 20 lbs. 12 oz., a loss of about 28 lbs., and it was still losing water when this paper was written. The interior of the root is fairly hard, yet quite porous, and very moist. Occasionally lateral roots give rise to new plants some distance from the mother plant. A few which were dug out had no roots of their own. They were dependent entirely on water and minerals conducted to them by the mother plant.

2. *Salsola pestifer* A. Nels. (Fig. 3) is the type of plant which occupies much of the soil around the margins of dunes. It seems to prefer the clay or gravel soils rather than loose sands.

FIG. 3. *Salsola pestifer* A. Nels.

It is characterized by a long slender tap root with relatively few large secondary roots. The longest tap root on any plant examined was 67 cm and the largest secondaries were slightly less than half this length. The basal diameter of the tap root on the largest plant was 5 mm. The roots branched out to the 4th category and root hairs were fairly abundant on the tertiary and quaternary divisions. The hairs varied from 140 to 160 μ long and were 6 to 7 μ in diameter.

3. *Solanum eleagnifolium* Cav. (Fig. 4) usually grows in shallow sandy areas where the ground is quite solidly packed, often in caliche, but occasionally it is found on the lower portions of dunes where there is considerable shifting sand. The plant has a deep-penetrating tap root. The longest tap root recovered was 114 cm with 32 large laterals of which 3 gave rise to new plants 40 to 60 cm away from the mother plant. The laterals which produced new plants were 10 to 16 cm beneath the surface in loose sand. At the base of the main plant there were 21 very small white roots from 5 to 8 cm long. The older roots were dark brown in color and only the largest laterals had tertiary roots arising from them. Hairs were abundant on all secondary and tertiary roots and averaged 120 μ in length and 8 μ in diameter.

FIG. 4. Long tap root of *Solanum eleagnifolium* Cav.

4. *Heliotropium convolvulaceum* (Nutt.) A. Gray grows abundantly on the shifting sands. The long slender tap root is white but as the plants get older the root becomes brownish. The longest tap root on any plant examined was 89 cm and it had a basal diameter of 6.5 mm. This

tap root produced only 12 secondaries and they had only 5 tertiary roots; these were on only two of the secondaries. The longest lateral was 34 cm long. Most of the laterals on this sparingly-branched tap root were either fairly near the surface or towards the distal end of the tap root. Twenty-seven cm of the central portion of the tap root had no laterals. Root hairs were sparingly distributed over the lower portion of the tap root as well as on the secondary and tertiary roots. *H. convolvulaceum* is a very successful dunes plant and typical of most species in this habitat; it would seem to have an inadequate root system for its water needs yet it always does remarkably well.

5. *Croton texensis* (Klotzsch) Muell. is found rather abundantly on the shifting dune sands. It develops a long tap root with numerous secondaries. The latter arise fairly uniformly about every 2 cm of tap root length. The longest tap root examined was 32.2 cm with a basal diameter of 3.5 mm. The largest secondary root was 15.0 cm long with a basal diameter of 912 μ. The tertiary roots averaged only 1.5 cm in length and 450 μ in basal diameter. The roots were yellowish-tan in color.

6. *Chrysothamnus nauseosus* (Pall.) Britton (Fig. 5) is the tallest of the shrubs growing in the dune area. It occasionally is over 4 feet but more commonly is 2 to 3 feet in height. The root system is characterized by an exceedingly long tap root and comparatively little branching. One plant removed from the side of a 12 foot high bank had a tap root that penetrated all strata listed in the early part of this paper and was still a comparatively large root as it continued on down. At the basal end this tap root was 3.6 cm in diameter and at the broken distal end, 391 cm (12′ 10″) down, it was 0.7 cm in diameter. The remainder of the root was not recovered. This entire root was unbranched except for one lateral which came off 137 cm beneath the surface. This branch also grew almost vertically and continued on through all the strata listed. Both roots grew through sand, several layers of gravel, and a clay hardpan layer.

This species was the only one to show the possible effects of extra moisture. The gravel layer which was present about 9 feet beneath the surface was somewhat more moist than any of the other layers. In this stratum numerous secondary roots were produced. These tiny secondaries (up to 5 cm long) were about 0.5 mm in diameter and from them tertiary roots appeared in abundance. The tertiaries were about 300 μ in diameter, but were only a few mm long. All of these

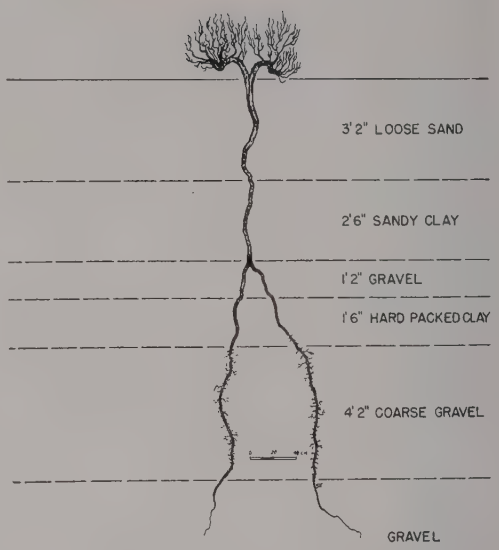

Fig. 5. Tap root of *Chrysothamnus nauseosus* (Pall.) Britton.

secondary and tertiary roots were covered with root hairs that averaged 210 μ long and 8 μ in diameter. The massed roots in this layer of coarse gravel which was 4 feet 2 inches thick were brown in color as were the hairs. No other stratum of soil above this gravel layer had any production of lateral roots nor did a gravel layer below have a similar development of roots.

7. *Franseria acanthicarpa* (Hook.) Coville is a widely spreading prostrate plant that occupies much of the loose sandy soil in the dune area. The roots are reddish brown to black and contain a good deal of tannin. The plant has a conspicuous tap root which is very deep-penetrating (Fig. 6). This root was quite fragile and difficult to remove intact. The longest we were able to dig out intact was 154 cm with a basal diameter of 5.2 mm. In most plants of this species examined there were many secondaries arising at the base of the plant and growing downwards in the upper 25 cm of surface soil. From that point downward there were few laterals arising from the tap root. *F. acanthicarpa* is a common host plant of the parasitic seed plant, broom-rape (*Orobanche multiflora* Nutt.). Often a very large broom-rape plant will be attached by but one root to a comparatively small host.

8. *Sphaeralcea parviflora* A. Nels. (Fig. 7) grows along the margins of the dunes usually with its roots in compact sand-clay. It becomes quite a large plant where water is adequate and the root system is correspondingly large. It has one

FIG. 6. *Franseria acanthicarpa* (Hook.) Coville showing massed surface roots and long tap.

large tap root and several major roots arising from the base of the plant. The tap root on one medium-sized plant examined was 80.4 cm long with a basal diameter of 3.8 mm. There were 16 secondary roots arising from this root, the longest of which was 72.5 cm. Tertiary roots were present on most of the secondaries, and root hairs, averaging 14 μ in diameter and 170 μ long, were present on the former.

Fibrous Rooted Plants

9. *Dalea scoparia* A. Gray (Fig. 8) grows freely in the loose sand with its long slender and sparingly-branched roots often extending over 20 feet radially from the base of the plant. It has a fibrous root system with 4 or 5 major roots growing laterally and one growing downward. It was observed that these lateral roots either grew downhill or laterally when the plant was growing on the slope of a dune. Most of the plants favored a downhill growth for their roots but the largest specimen examined had a few roots growing slightly uphill also. The root system of one medium-sized individual consisted of two major roots arising from the base; one grew vertically, the other laterally. Each of these roots

FIG. 7. *Sphaeralcea parviflora* A. Nels.

gave rise to one major lateral within the upper 12 cm of its length. These 4 roots thus formed the basis for the root system. The large root that grew vertically had a basal diameter of 23 mm and extended downward to a depth of 152 cm. It had 18 secondaries arising from it and only 2 of these laterals produced one tertiary root apiece.

The second large root had a basal diameter of 14.5 mm and extended 123 cm. One of the long laterals which arose near the base of the plant had a basal diameter of 8.2 mm and extended 278 cm in length. The second large lateral was 9.0 mm in basal diameter and 185 cm long. There were four tertiaries arising from this root of which the largest was 30.9 cm long.

The dimensions given were the most complete for any of this species examined but they were not from the largest plant studied. The largest one had one root 670 cm long. The remarkable characteristic of the root system of this species is

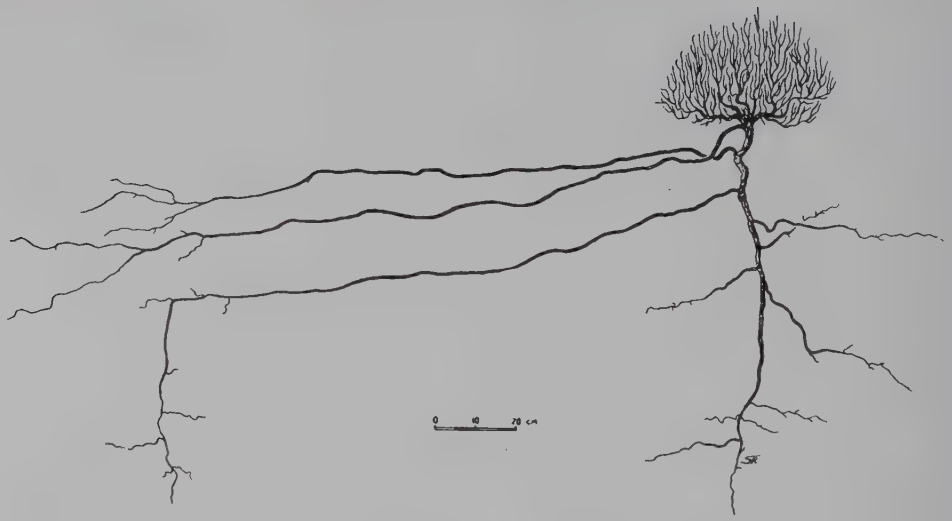

FIG. 8. Fibrous root system of *Dalea scoparia* A. Gray.

its paucity of lateral roots. All major roots had several feet of length without lateral root development. One of the major lateral roots on this plant extended 171 cm before it produced a lateral.

10. *Artemisia frigida* Willd. had a completely fibrous root system with many shoots arising from horizontal rhizomes. The individual shoots arise about every 12 cm along the branching rhizomes and form a clone of many plants. The adventitious roots arising from the rhizomes are of two types, based on size. The larger ones arise about every cm of rhizome length. These roots are dark brown to almost black in color. The smaller roots arising from the rhizomes are grayish in color and are about 1½ times as numerous as the larger ones. Secondary roots arise from both types of roots and are fairly well covered with root hairs. The hairs average about 300 μ in length and are 11 μ in diameter.

11. *Oryzopsis hymenoides* (Roem. and Schult.) Ricker is a clump grass which grows very widely along the margins of the dunes. Each year new shoots are produced around the old ones from short rhizomes. Comparatively few roots are produced on the plants until the "rainy" season which begins in July. Our latest collection of this species was August 1. At that time the old main roots on the plants were 30 to 45 cm long and averaged about one main root to a shoot. Numerous short white roots less than 2 cm long were beginning to develop. These replacement roots were 4 times as numerous as the old roots. The older main roots had many secondary roots arising from them but these secondaries were quite short. They were all less than 6 mm long and none had tertiaries. Root hairs were present but comparatively sparse.

12. *Cenchrus pauciflorus* Benth. is a clump grass which increases in size by means of short rhizomes giving rise to additional shoots within the clump. Our latest collection of this species was August 1. The main roots were more numerous than those of *O. hymenoides* and similarly about 4 times as many new roots were developing from the base of the shoots. These new roots were from 2 to 5 cm long while the older main roots were from 25 to 35 cm long. Numerous secondary roots were present on the main roots and were less than 1 cm long. Tertiary roots were beginning to form on a few of the secondaries but were mere protuberances at this time. The main roots were well covered with root hairs. *C. pauciflorus* had the same habitat as *O. hymenoides* but seems to be preferred by cattle much more than the latter.

13. *Opuntia arborescens* Engelm. does not grow directly on the sand dunes but is rather commonly found on the margins in the more compact sandy clay soils. It is one of the few plants not characterized by a prominent tap root. The roots are light brown in color, fibrous, and heavily massed in the upper 18 inches of soil, a few slender roots are occasionally found as much as 3 feet beneath the surface but the great majority are surface roots. One plant had a root within the upper 3 inches of soil which trailed off laterally for 338 cm (11 feet). The root had a basal diameter of 1.3 cm and a distal diameter of 4 mm

where it was broken and the remainder of the root was not recovered. Arising from this long root were 27 secondaries which varied in diameter from less than a mm to 3.5 mm. These roots grew downward rather than laterally. A second long surface root trailed off laterally 220 cm with 30 secondary roots arising from it. Many of the secondary roots had tertiaries arising from them and a few of these had short quaternary roots. Hairs were abundant on roots of the secondary and tertiary categories. They averaged just 4 μ in diameter and about 180 μ long.

The roots of all species were examined for mycorrhizae and nodules. Many of the species had a few fungus hyphae in close association with the hairs and smaller roots but the number was extremely small in comparison with the mycorrhizae of plants growing in more fertile soils. *Dalea scoparia,* even though a legume, did not have bacterial nodules associated with its roots, nor were any present on the other species.

Discussion and Conclusions

There are many reasons for studying the root systems of different plants in similar and various habitats. The aim in this investigation is a better understanding of the rooting habits of certain arid-dwelling plants and to determine whether the characteristics of these plants warrant an attempt at classification. Most botanists are content to classify root systems as tap or fibrous, but the individual differences which exist between the different species is such that one familiar with the root systems of a number of plants can recognize many of them by their root systems alone. Although many investigators ascribe these differences to the edaphic environment, there are strong inherent genetic factors which unquestionably contribute to the characteristics of the root system.

How susceptible roots may be to modification, through a variation in the soil medium or its water content, has yet to be determined. Our own observations are that inheritance is a powerful influence and the type of root system typical of the species will remain essentially the same under whatever conditions it may be found. Obviously there are extremes in environmental situations which might greatly modify a root's gross morphology. The bare rock substrate of a lava flow provides a stark environment for most roots, yet within the cracks of broken rocks and bubbles of vesicular basalt enough soil will blow in to provide a stringent habitat for growth. Even here the characteristic root system is developed insofar as possible, but the rocky environment limits the extent of lateral spread expected of many of these species and forces them into extensive vertical growth.

The root systems of the plants described in this investigation were either tap or fibrous and in two species a combination of both. Deeply penetrating tap roots were the most common and because of the few roots found on many of the plants it is unlikely that much in the way of water storage facilities was available to them. The exception to this is, of course, the highly distinctive tap root of *Ipomoea leptophylla* which forms a large bulbous reservoir near the upper portion of the main root.

Most of the work on desert plants has been concentrated on the various modifications of the aerial parts which are subjected to desiccating winds and intense heat. The reactions of the roots to desert conditions have, to a large extent, been neglected. Yet the soil is a most important feature of the plant's environment and only through this medium are the water and mineral needs of the plant met to sustain life. The roots, therefore, occupy a place of preeminent significance to the plant for they penetrate a substrate that is always changing, both chemically and physically, and to which they must adapt themselves in form and structure. It is not our purpose to discuss the physiological relationships which the plant has to its environment but rather to consider the gross morphology of the subterranean plant parts.

The plants in this investigation varied to a limited extent in their types of root systems. All had at least one root that penetrated to a depth of at least 3 feet except the grasses, which produced numerous fibrous roots in the upper foot of soil with a few of the slender organs penetrating into the second foot. *Artemisia frigida* falls very much in this same pattern. The numerous adventitious roots are heavily concentrated in the upper foot of soil with relatively few of the older roots going much deeper.

Effect of Competition

Aside from the fact that most of the dicotyledonous plants have prominent tap roots, the greatest similarity among all species was the relatively little branching of the roots. One factor which may limit the lateral spread of mesophytic plants is the close proximity to others of the same or different species. Plants of arid habitats usually grow comparatively far apart and therefore do not have the competition for space associated with plants of less severe environment.

In previous studies (Dittmer 1937) it was found that winter rye when growing singly, without competition, produced numerous roots to the

quaternary division, but when this plant was growing in the field (1938) in close proximity to other rye plants, it did not branch beyond the tertiary division. This situation has been found true of other plants also. However, the plants growing on and at the margins of the dunes in this study were sufficiently far apart that competition could not have retarded the degree of branching. Obviously a factor or factors other than competition limited the production of lateral roots. Most of the plants in this study had tap roots of considerable lengths where no secondaries had formed and relatively few of the secondaries produced tertiary roots.

Effect of Water

The environmental factors of great temperature variations, low humidity, and desiccating winds exert a profound influence on the aerial portions. Such modifications as the presence of trichomes and spines, the reduction of the transpiring surface, orientation of leaves, double epidermis, tightly compacted leaves, heavy outer cell walls or cutinized surfaces and other variations have been long associated with arid and semi-arid plants. Yet these modifications are not confined solely to plants of these regions but in them may find a more complete expression. Unlike the shoot, however, there is no "xeric" type of root system unless the meager branching of the roots and the deep-penetrating and widely dispersed laterals may be associated with this habit. It might be concluded that *I. leptophylla* has a typical xeric type of root, yet it is not like the other successful plants in the area. It may be "ideal" but it is not "typical." Certainly roots of different character, whether fleshy or fibrous, sparse or copious, deeply penetrating or shallowly superficial, are not affected in a manner analogous to the shoots. It would be difficult, if not impossible, to look at a root system and say that it is "typical" of an arid habitat. Still the root systems described for the plants in this investigation do have a few similar characteristics. These roots are very much elongated, sparingly branched with very small hairs confined to the smallest roots. The differences in the plants are very likely much more of a physiological nature, as compared to mesophytic species, than of a morphological character.

That water does have some influence on the extent of root development has been observed by a number of investigators. Conrad and Veihmeyer (1929) contend that moisture in the soil influenced root development but if the soil is wet at the beginning of the growing season to the full depth to which roots would normally penetrate, subsequent additions of water by rain or irrigation had but little influence on the extent of the root system developed.

Experiments by Hendrickson and Veihmeyer (1931) indicate that sunflower roots would not extend more than a few millimeters into dry soil but Shantz (1927) believes that some drought resistant plants do have the ability to push through dry soil where ordinary field crops would fail to do so. This opinion is also shared by Breazeale (1930). He concluded that roots will elongate into dry soil because of the "build-up" of the moisture content of the dry soil by water transported from the roots in moist soil.

Kramer (1940) concluded that the great amount of root growth made by certain plants was capable of handling the day to day water needs of the plant even though the remainder of the root system was no longer a functional absorptive organ. This may be true also of the widely dispersed roots of the plants examined here. If it is true, the water needs of such a plant must be at a minimum compared to those of more favorable habitats, since its new growth is comparatively small. It is also possible, although unlikely, that the roots of these plants can take in water at a faster rate than those of other plants. Certainly the roots of the older plants examined were highly suberized and often corky. We may assume that little water is taken in through these heavily suberized walls, yet it is possible a certain amount of imbibition might occur which will ultimately place some water in the conductive channels.

One would expect with the amount of shoot development and number of leaves produced by these plants that the number of roots and root hairs would have to be much more extensive than that found. We may assume that these plants either lose very little water by transpiration or that the few roots present are highly efficient absorptive structures. None of the plants had above-ground parts which were modified for water storage, although the canes of *Opuntia arborescens* were quite fleshy and held considerable water.

Effect of Hardpan

Weaver and Crist (1922) observed that native species such as *Opuntia polyacantha* Haw. and *Psoralea tenuiflora* Pursh. penetrated a hardpan layer and often formed the bulk of their root system below this hard layer. They also commented that *P. tenuiflora* had the same root habit whether the plant grew in dry or moist situations. In the present study, most plants were growing

in a uniform soil of sand. Occasionally some roots penetrated a calcareous hardpan fairly near the surface but for the most part the depth of the sand was such that the roots had a completely uniform medium in which to grow. Consequently the physical structure of the soil as well as water content was quite uniform. One specimen of *C. nauseosus* grew through six different strata, including a hardpan layer, with no change in direction of growth or degree of branching except in one moist gravel layer where numerous secondary roots appeared from the outer tissues of the old root (Fig. 5). The root portions in the strata below and above this gravel layer did not have similar secondary root development.

Summary

A study was made of the subterranean plant parts of 13 species growing in the sand dune area near Santa Ana Pueblo, New Mexico. Counts and measurements were made on the root systems of 82 plants.

Eight species developed tap root systems and 5 were fibrous rooted. Two of the plants with long tap roots also developed numerous roots in the upper soil levels.

Most of the plants had their roots confined to the soft sand layers although a few grew deep enough to penetrate the hardpan caliche stratum.

Most of the plants in this study had comparatively few laterals when compared to other plants of more mesophytic environments.

It was impossible to state that any one type of root system was more successful or better adapted to a xeric environment than any other.

Within the narrow range of the habitat conditions in this study, variations in the root system of the different species cannot be attributed to the environment. Other factors, possibly genetic, undoubtedly play a more prominent role in determining the type of root system and the degree of branching than the environmental factors present here.

Root hairs were present on the small roots of all plants examined. These hairs were quite small compared to those of many other species but size of hairs is characteristic of any given species rather than determined by environmental influences.

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TRICKLING FILTER ECOLOGY

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Introduction

According to Clarke (1954), "the fundamental steps in the operation of an ecosystem are: (1) reception of energy; (2) production of organic material by producers; (3) consumption of this material by consumers and its further elaboration; (4) decomposition to inorganic compounds; and (5) transformation to forms suitable for the nutrition of the producers. If the area is occupied by a self-sufficient community, all these steps will go on within it."

On a large scale, and on the basis of a large population of microscopic or near-microscopic organisms, a trickling filter embodies many of the characteristics of the independent ecosystem as outlined above. However, the trickling filter is

a man-made ecosystem and few man-made ecosystems are truly self sufficient. The trickling filter is built for one purpose, the treatment of sewage by the action of a biota upon it. This biota is independent only as long as sewage is applied to the filter. The development of such a biota is relatively rapid. Its members are derived from the population of surrounding soils, waters, or habitats in which decaying or decomposable materials are present, as well as from sewage.

Basically the trickling filter population is composed of decomposers, transformers, and locally, of producers which are partly dependent on the other members of the biota.

Habitat

In the United States today there are three principal methods of sewage disposal. One of the commonest is the direct release of polluted water into the nearest stream. A refinement on this process is found in the primary treatment of sewage in which the sewage is directed into settling basins with or without the addition of chemicals. After settling out of solid materials, the liquid is added to that of the nearest stream. However, purification (removal, by natural or artificial methods, of objectionable matter from water) usually results in only 25%-40% BOD removal and approximately up to 70% suspended solids removal. The biochemical oxygen demand (BOD) of sewage is the quantity of dissolved oxygen, in mg/l, required during stabilization of the decomposable organic matter by aerobic biochemical action (Standard Methods, 1955). A further refinement is effected by any one of several biological treatment processes, commonly through the use of activated sludge or trickling filters. A sanitary engineer whose duties include maintenance of a sewage treatment plant thus becomes a biological engineer using tools of applied ecology.

A number of terms to be used in the description of trickling filters may be defined according to the Glossary of Water and Sewage Control Engineering (1949) for a clearer understanding of some of the problems to be discussed. In the following discussion, quoted terms and definitions are from this source. The broadest definition of sewage is "the water supply of a community after it has been fouled by various uses." This may be broken down into the two most important types of pollution, domestic or sanitary sewage and industrial wastes. The latter may be processed in special treatment plants, or in conjunction with domestic sewage in municipal plants of the primary or secondary type. The municipal treatment plant operator usually is concerned with the former although he realizes that some industrial wastes are included.

The operation of a secondary sewage treatment plant is based on one or another method of "biochemical-," "biological-," or "sewage oxidation," a . . . "process whereby, through the agency of living organisms in the presence of oxygen, the organic matter contained in sewage is converted into a more stable or a mineral form." Among the principal techniques of exposing sewage to the oxidative actions of microorganisms are the activated sludge process and the trickling filter. The latter is the only method with which we are concerned in this report. The anaerobic digestion of sludges is not considered here.

In the literature of sewage purification a number of terms have been used to describe the trickling fileter. This structure is defined as follows: "A filter consisting of an artificial bed of coarse material, such as broken stone, clinkers, slate, slats or brush, over which sewage is distributed and applied in drops, films, or spray, from troughs, drippers, moving distributors, or fixed nozzles, and through which it trickles to the underdrains, giving opportunity for the formation of zoogleal slimes which clarify and oxidize the sewage." The process is termed "biological filtration." The structures have been termed "bacteria beds," "contact beds," and "percolating filters." The modification in which the spray comes from fixed nozzles has been termed a "sprinkling filter." Depending on the rate sewage is applied to the filter after primary settling, the filter may be termed "high-rate" (dosed at 10-30 million gallons per acre per day—mgad), or "standard-rate" or "low-rate" (dosed at 1-4 mgad). Since the Orford Subcommittee (1957) prefers the use of "low-rate" to "standard-rate" this term is used in the following discussion. Other modifications of the trickling filter are in use but the work on which this report is partly based has been done on low-rate and high-rate trickling filters.

As indicated above, the trickling filter exists to support a biological community referred to as a "zoogleal slime." This has been referred to commonly as a "microbiological film" which is defined as "the gelatinous film of zooglian growths covering the media or spanning the interstices of a biological bed." "Zoogloea," in the terminology of sewage treatment, is defined as a "jelly-like matrix developed by bacteria. The word is usually associated with activated sludge growths in biological beds." The bacteriologist is more specific in his use of this term. To him *Zoogloea* is a distinct genus of bacteria, as well as the type of bacterial growth produced during certain phases

of the life cycle of single, colonial, or filamentous bacteria which can produce gelatinous matrices.

Finally, the term "degree of purification" may be mentioned. This phrase is defined as "a measure of the removal, oxidation, or destruction of solids, organic matter, bacteria or other specified substance effected by sewage treatment processes." The degree of purification of sewage represents the efficiency of the sewage treatment plant. This rating can be used as a means of obtaining more funds with which to build a more efficient plant, or as a means of evaluating the residual waste products of a municipality which are being emptied into streams. The purity of such water is important to other communities downstream and to the biota of the stream.

The trickling filters studied most intensively by the writer are those in the Dayton, Ohio, sewage treatment plant. This plant is primarily concerned with the treatment of domestic sewage. The conditions of the influent are relatively constant since only rarely do loads of industrial wastes exceed the capacity of the plant to handle them with the domestic sewage. Eight of the 20 filters are of the high-rate type and are dosed continuously throughout the year. The remaining 12 filters are of the low-rate type and receive the excess portion of the settled sewage. Their dosage is, therefore, essentially, intermittent, occurring only during periods of the day when the plant is receiving peak loads. Living conditions for the biota of the low-rate filters are different from those of the high-rate filters. Data on effectivity of operation of the two types are not available since effluents are composited before analysis.

The filters are 165 feet in diameter, 7.5 feet deep, constructed in the form of a concrete cylinder with a funnel-shaped channeled base, and are filled with more than 160,270 cubic feet of limestone slag. On the porous surface of this rock a population of microorganisms has developed. Because it is impractical to dig deeply into this mass of rock, which varies in size between two and five inches in diameter, only the surface layer of stone has been examined periodically and regularly.

Since the habitat is man-made, and since it was made for a specific purpose, it is reasonable to expect that conditions in the habitat will be modified from time to time to increase the efficiency of the structure and its population. The most noticeable effects on the filter biota are produced by alteration of dosing rates, when the filters are shut down for repairs or when excessive run-off from precipitation dilutes the sewage.

Effects of changeable air temperature on the filter surfaces are ameliorated by the relatively constant temperatures of the continuous dosage of settled sewage.

Relatively little ponding occurs in the filters. Spaces between the stones are large enough in most cases so that cross growth has not occurred and the filters are well ventilated. Conditions of excessive septicity rarely, if ever, develop.

Biotic effects of the population appear to be relatively constant. If disseminules of additional species reach the site and the species becomes effective in the population, little change will result since the new species will have replaced a species unable to maintain the competitive level. However, it is not to be implied that numbers of species are fixed. Effects of various groups of species in the population are relatively constant since they are apparently controlled by interaction and available food supplies. A possible exception could be found in seasonal over-population of snails or worms neither of whose influence is reflected in the activities recorded in the weights of material found on sampling slides or in species or colonies of organisms isolated therefrom.

Populations

Introduction

The biotic populations of the trickling filter are relatively uniform in composition. That is, bacteria, fungi, protozoans, algae, nematodes, rotifers, snails, sludge worms, and larvae of certain insects of which the foregoing are composed, may vary from filter to filter, at the species level, but the biota, whether the filter is in the United States or in Europe, remains relatively constant. Occasionally, when conditions permit, other organisms may also be found such as the mosses reported at Dayton (Cooke 1953). Such organisms are accidental invaders, are restricted to marginal areas, and rarely complete their life cycle, remaining in the vegetative state.

In the past identification of the members of this population has been of little concern to the sanitary engineer as long as the population became established and functional relatively quickly after placing a filter in operation. A good operating condition is one in which little clogging occurs in the spaces between stones and one which carries on its function of removing solid, colloidal, or dissolved materials from the sewage, thus reducing its biochemical oxygen demand.

The presence of bacteria has been considered normal. The species which are present have not been evaluated beyond the requirement that the coliform content of final sewage discharged into

the receiving stream be low or lacking. Fungi have been considered nuisances more than aids in the biological treatment of sewage (Becker 1954; Cooke 1954). Tomlinson in England (1941, 1946) has found that several species of fungi are members of the population, as have Hesseltine (1953) and Cooke (1957). On the other hand, Becker and Shaw (1955) report that the occurrence of fungi is seasonal and of little significance. Lackey has surveyed the protozoan populations (1924) in New Jersey while intensive population studies have been carried on with these organisms in England. The occurrence of algae has been noted occasionally according to a survey of Stanbridge (1955). His finding seems odd since algae are invariably present on the surface of trickling filter rock in the many filters which have been observed by the writer. Insect populations have been studied in England relatively intensively (Hawkes 1952), because certain species have become nuisance problems in that country discovery of control methods has appeared to be important. Recently problems of snail control have been considered by Ingram *et al.* (1958) in connection with equipment damage and nuisance problems.

Composition of Microbial Film

To date, few comprehensive studies have been published in which the biota of the zoogleal slime has been described. Bacteriologists, mycologists, algologists, entomologists, or protozoologists have been interested in one filter or another, at the surface or more rarely at several depth levels, and have reported on their observations without overlapping into the interrelated fields. Occasionally a few organisms from one or more of the other members of a population have come to the attention of the observer but the resulting lists are incomplete. Consequently, a composite list of organisms is presented to indicate the complexity of the populations on the trickling filter. It would be difficult for one individual to study the whole population and its interrelationships comprehensively since the organisms involved cover such a wide range of groups of species in plant and animal kingdoms.

A report by Heukelekian and Crosby (1956) includes relatively representative chemical and physical data on the composition of zoogleal slimes. Since it is difficult to get materials by direct scrapings from trickling filter stone, unglazed tiles were exposed in channels carrying sewage to obtain slime growths of similar composition to those found on trickling filter stones. Table I indicates the type of physical and chemical data of interest to the sewage treatment plant operator.

TABLE I. Analysis of slimes (after Heukelekian and Crosby, 1956)

Determination	Results
pH	8.6
Density at 20° C	1.0122
Moisture, % of wet weight	95.4
Total solids, % of wet weight	4.6
Volatile solids, % of total solids	70.7
Ash, % of total solids	29.3
Total nitrogen, % of total solids	1.0*
Ammonia nitrogen, % of total solids	0.5
Grease, p.p.m.	15.7

*This determination is low for a mass of organisms but materials on which the determination was based include sludges and other inert matter which would tend to reduce the ratio of nitrogen to other elements present.

In studying the populations of the sewage treatment plant and its included processes, the bacteriologist is interested primarily in the occurrence of coliform bacteria. This group has long comprised one of the most important groups of organisms indicative of sewage pollution (Kabler 1957). High coliform density indicates a high degree of pollution. One requirement of effective sewage purification in some communities is the removal of as many coliform bacteria as possible. Thus, beyond routine checks of m.p.n. (most probable number) of coliform bacteria, whether done by the STANDARD METHODS (1955) or the membrane filter (Clark *et al.* 1951) tehnique, little attention is paid at present to other kinds of bacteria present on trickling filters. No comprehensive species lists have been found in the literature for this habitat. However, Hotchkiss (1924) prepared a list of bacteria by their activities on sprinkling filter beds in New Jersey. An average of 20-24 samples obtained throughout the year gave the following numbers of bacteria in thousands per cc. of filter slime; nitrate reducers 208.4, H_2S producers (from protein) 172.9, albumen digesters 102.6, species which oxidize nitrites to nitrates 53.3, species which oxidize NH_4 salts to nitrates 39.8, H_2S producers (from sulfates) 19.1, and species which reduce thiosulfate to sulfate 2.0.

As early as 1914, Johnson, in England, observed bacteria and fungi on filters. He considered that *Sphaerotilus natans* was among the important bacteria on the beds he studied and that it took the form of *Zoogloea ramigera* and its varieties *compacta, carnea,* and *uva* under certain circumstances of growth. The review of the literature on the fungi of sewage by Cooke (1954) indicated that *Sphaerotilus natans* is widespread in sewage and polluted water, that it is known in

several forms referred to in the literature as species and even genera, and that it can assume a zoogloeal stage in its life history. Johnson reported on the appearance of seven fungi on trickling filters but the nomenclature he used, while probably valid at that time, refers now to such different organisms, or organisms listed today under such different names, that to repeat them would only add to confusion.

In studies on the fungus populations of trickling filters, both in connection with the technique of sampling such habitats with glass slides (Cooke 1958) and with sampling the populations by scraping the slime from stones (Cooke and Hirsch 1958), 90 species of fungi have been presented. Of these more than 20 species are considered to be members of the permanent population of fungi found on trickling filters.

During much of the year the trickling filter is covered with a green film of algae. This is only one of the several types of organisms in the slime on the upper or surface layers of stone. Except for those algae which are washed down through the filter and somehow manage to survive, these organisms are limited in distribution to those portions of the filter exposed to the light. Early listings included the genera *Chlorella, Stigeoclonium, Euglena, Phormidium,* and *Oscillatoria* without regard to the species represented. In a recent paper by Cooke and Hirsch (1958), the following species were listed from the Dayton, Ohio, trickling filters: *Nitzschia palea, Stigeoclonium nanum, Ulothrix tenuissima, Characium* sp., *Chlorococcum humicola, Chlorella vulgaris, Phormidium uncinatum, Amphithrix janthina, Anacystis montana,* and *Pleurocapsa* sp.

It was found that high-rate and low-rate filters supported different populations of algae especially when loadings were distributed over different periods of time. At Dayton, the high-rate filters receive settled sewage continuously throughout the 24 hours of the day while the low-rate filters received only that in excess of the high-rate filter capacity. Where leakage occurred around the base of the column supporting the distributor arms, the pattern of slime growth is similar on both filters. Diatoms and green algae predominated on the high-rate filters while blue-green algae were abundant on the low-rate filters.

Extensive work on the protozoan and other animal life in the sprinkling filter beds at Plainfield, New Jersey, was published by Lackey (1926). During the course of his study it was found that 19 rhizopods (Sarcodina) occurred in the microbial film on the filter stones. Stones from 1-, 3- and 5-foot depths were examined and the commoner species quantitated. The following rhizopod species were listed: *Actinophyrys sol, Actinosphaerium eichhornii, Amoeba proteus, A. radiosa, A. verrucosa, Arcella dentata, A. vulgaris, Centropyxis aculeata, Chlamydophrys stercorea, Cochliopodium bilimbosum, Difflugia pyriformis, Euglypha alveolata, Hartmanella hyalina, Pamphagus nutabilis. Protamoeba primitiva, Trinema lineara, Vahlkampfia albida, V. guttula,* and *V. limax.* Lackey's earlier paper on filter bed protozoans in New Jersey (1924) listed the following genera of rhizopods as including the commoner species: *Amoeba, Arcella, Difflugia, Euglypha,* and *Trinema.*

In addition to work on rhizopods, Lackey (1924) listed the various genera of flagellates and ciliates which occurred on New Jersey filters. In addition to "small flagellates" in the Mastigophora, the genera, *Distigma, Euglena, Heteronema,* and *Notosolenus* were listed as including at least one species each. In most work with rhizopods, flagellates, and ciliates in the United States the organisms are listed only according to genus. Such listing indicates a lack of interest in identification below the generic level, or difficulties in making specific identifications which would require more time than is available for this type of study.

The genera of ciliates (Infusoria) as listed by Lackey (1924) included: *Opercularia, Aspidisca, Blepharisma, Chilodon, Colpidium, Frontonia, Lembus, Lionotus, Metopus, Oxytrichia, Paramoecium, Pleuronema,* and *Vorticella.* In 1926, Lackey added to this list some genera of less common occurrence: *Prorodon, Macrymaria, Holophrya, Nassula, Chilodon, Loxodes, Loxophyllum, Amphileptus, Lionotus, Lionotopsis, Glaucoma, Uronema, Colpoda, Colpidium, Microthorax, Lembus, Cyclidium, Pleuronema, Paramoecium; Stentor, Blepharisma, Metopus, Spirostomum; Uroleptus, Amphisia, Oxytrichia, Stylonichia, Euplotes, Aspidisca; Opercularia, Vorticella,* and *Carchesium.* In the Suctoria, only the genus *Podophrya* was listed. Butcher, in England (1932), has indicated the importance of *Carchesium, Vorticella* and other stalked ciliates in the biota of sewage by listing them among the organisms commonly called "sewage fungus." Butterfield, Purdy, and Therriault (1931) advanced a theory of the place of these organisms in sewage treatment following a series of experiments at Cincinnati. They stated that . . . "the chief function of certain plankton (*Colpidium,* a ciliate) in the biochemical oxidation process is to keep the bacterial population reduced below the saturation point and thus to provide conditions

suitable for continuous bacterial multiplication, thus in turn resulting in more complete oxidation." Therefore, certain protozoans are seen in both activated sludge and in trickling filter slime as browsing or grazing organisms which may remove some solid, colloidal, or dissolved organic materials, but which primarily aid in the control of the bacterial populations. In some cases, yeast cells may be ingested also but the protozoan organisms are usually too small for effective control of the yeast population.

In a study of the biology of sewage in the Brent and East Ham sewage treatment plants in England, Peters (1930a) listed the protozoans and other animals found throughout the treatment plants. He did not indicate which organisms were found in the trickling filters although 39 of the 52 categories listed were found in them.

Peters (1930b) was especially interested in the nematodes occurring in sewage treatment plants in England. The species *Diplogaster strictus, Diploscapter coronata, Dorylaimus saprophilus,* and *Rhabdites* sp. were listed. Workers in the United States, such as Lackey (1924) and Wilson (1943), are content to list nematodes only as a group category without attempting to resolve the populations into the various genera and species which are present. These are among the larger microscopic animals in trickling filter film and any mount will include some individuals.

Among other members of the animal populations of the sprinkling filters at Plainfield, New Jersey, Hausman (1923) listed unidentified nematodes, rotifers, annelid worms including *Aeolosoma* and *Pristina,* and *Tartigrada.* Combined counts at three levels in thousands per cc. of centrifuged film showed some seasonal variation in the occurrence of these organisms.

In 1939, Reynoldson made a very thorough study of (enchytraeid) segmented worms in bacteria beds in England. The most important species was considered to be *Lumbricillus lineatus* while *Lumbricus rubellus* was also abundant. Usually adults were found at lower levels while the young were near the surface. Their feeding habitats were closely associated with the growth of *Phormidium* sp. on the surface film. Drying conditions in summer and cold temperatures in winter tended to send these animals deeper into the filter beds. The cycle of their appearance indicated that they were responsible for sloughing. As the algae returned after 3-4 weeks the worms moved upward to feed upon this growth. The more rapid regeneration of the algae in the summer was also attributed to the effects of the worms. The value of the worms in developing sloughing conditions and in controlling the film was demonstrated experimentally. In the filters under study the worms were considered as important as the insect larvae, *Psychoda severini, P. alternata. Metriocnemus longitarsus, M. hirticollis,* and *Spaniotoma minima,* in controlling accumulative film growth. The snail, *Limnea glabra,* as well as mites and spiders also occurred on these filters.

Wilson (1943, 1949) reported that scouring organisms such as *Macrobiotus* sp., oligochaete worms, and insect larvae were important in preventing excessive development of film and increasing plant efficiency in Wisconsin and Minnesota. The worms listed included: *Aelosoma hemprichi, Pristina* sp., and *Dero* sp. He stated that while worms such as *Dero* were few in number they exerted a potent influence on the reduction and stabilization of sewage solids and assisted in clearing voids between rocks to the improvement of ventilation.

Imhoff and Fair (1956) indicated that among the worms present in trickling filters were the "aquatic earthworm" *Limnodrilus* sp., and the reddish bristle or sludge worm *Tubifex* sp.

Usinger and Kellen (1955) studied the role of insects in several types of sewage disposal beds in California. In an experimental biofiltration plant at San Rafael Meadows insect larvae were found. The commonest species was a member of the Diptera, *Psychoda alternata.* Other Diptera included: *Limonia simulans concinna, Diploneura cornuta, Scatella stagnalis, S. paludum,* and *Leptocera fontinalis. Cercyon fimbriatum,* a member of the Coleoptera was also found.

An experimental lath filter was set up in Iowa for the treatment of milk wastes. Frye and Becker (1929) studied the fauna of the slimes which developed on the lath at 1-foot intervals in the 6-foot deep filter. The organisms were presented in a combined list with the protozoans qualified as "common" or "rare." The list included: Protozoa: Sarcodina: Common: *Dimastigamoeba gruberi, Vahlkampfia linas, V. albida, Amoeba* sp., *A. radiosa, Euglypha alveolata, Chlamydophrys* sp., *Actinophrys sol, Centropyxis aculeata,* and *Arcella vulgaris;* Rare: *Amoeba* sp., *A. proteus, A. verrucosa,* and *A. villosa;* Mastigophora: Common: *Monas* sp., *Cercobodo ovatus, C. longicaudata, C.* sp., *Bodo caudatus, B. lens, Distigma proteus, Peranema trichophora,* and *Trepmonas agilis;* Rare: *Mastigamoeba* sp., *Oicomonas socialis, Bodo mutabilis; Euglena* sp., *Anthophysa vegetans,* and *Tetramitus* sp.; Infusoria: Common: *Chilodon cucullus, Colpoda* sp., *C. inflata, Cinetochilum margaritaceum, Linotus*

TABLE II. Composite list of trickling filter organisms

(Genera in major groups listed alphabetically regardless of importance or systematics)

Schizomycetes (bacteria)
- Sphaerotilus natans
- Zoogloea ramigera
- Many unidentified species

Cyanophyceae (Blue Green Algae)
- Amphithrix janthina
- Anacystis montana
- Oscillatoria limosa
- Phormidium uncinatum
- Pleurocapsa sp.

Eumycophyta (Fungi)
- Absidia corymbifera
  - cylindrospora
- Allescheria boydii
- Alternaria tenuis
- Ascodesmis microscopicum
- Aspergillus spp.
  - candidus
  - clavatus
  - flavipes
  - flavus
  - fumigatus
  - niger
  - ochraceous
  - sydowii
  - terreus
  - ustus
  - versicolor
  - wentii
- Cephalosporium spp.
- Chaetomium globosum
- Cladosporium cladosporioides
- Coniothyrium spp.
  - fuckelii
- Dematiaceae spp.
- Epicoccum nigrum
- Fusarium spp.
  - aquaeductuum
  - oxysporum
  - roseum
  - solani
- Geotrichum candidum
- Gliocladium roseum
- Gliomastix convoluta
- Leptomitus lacteus
- Margarinomyces heteromorphum
- Memnoniella echinata
- Monilia sitophila
- Moniliaceae spp.
- Mucor sp.
  - fragilis
  - plumbeus
  - racemosus
  - saturninus
- Myrothecium verrucaria
- Paecilomyces varioti
- Penicillium spp.
  - brevi-compactum
  - chrysogenum
  - clavigerum
  - cyclopium
  - digitatum
  - expansum
  - funiculosum
  - herquei
  - implicatum
  - janthinellum
  - lilacinum
  - ? luteum
  - martensii
  - nigricans
  - ochro-chloron
  - oxalicum
  - palitans
  - piscarium
  - purpureogenum
  - roquefortii
  - stipitatum
  - variabile
  - velutinum
  - vermiculatum
- Phoma spp.
- Pullularia pullulans
- Rhizopus spp.
  - arrhizus
  - nigricans
  - rhizopodiformis
- Rhodotorula spp.
- Sphaeronema spinella
- Sporotrichum pruinosum
- Stachybotrys atra
- Stemphyllium consortiale
- Subbaromyces splendens
- Syncephalastrum racemosum
- Trichoderma viride
- Trichothecium roseum
- Verticillium spp.
  - lateritium
- White yeasts

Chrysophyceae (Diatoms)
- Nitzschia palea

Chlorophyceae (Green Algae)
- Aeronema polymorphum
- Characium sp.
- Chlorella vulgaris
- Chlorococcum humicola
- Microthamnion kuetzingianum
- Richteriella sp.
- Stigeoclonium nanum
- Ulothrix tenuissima

Bryophyta—Musci (Mosses)
- Leptodictyum riparium

Protozoa
- Sarcodina (Amoeboid organisms)
  - Actinophrys sol
  - Actinosphaerium eichhornii
  - Amoeba proteus
    - radiosa
    - verrucosa
    - villosa
  - Arcella dentata
    - vulgaris
  - Centropyxis aculeata
  - Chlamydophrys stercorea
  - Cochliopodium bilimbosa
  - Difflugia pyriformis
  - Distigamoeba gruberi
  - Euglypha alveolata
  - Hartmanella hyalina
  - Pomphagus nutabilis
  - Protamoeba primitiva
  - Trinema lineare
  - Vahlkampfia albida
    - guttula
    - limax
- Mastigophora (flagellates)
  - Anthophysa vegetans
  - Bodo caudatus
    - lens
    - mutabilis
  - Cercobodo sp.
    - longicaudata
    - ovatis
  - Distigma proteus
  - Euglena sp.
  - Heteronema sp.
  - Mastigamoeba sp.
  - Monas sp.
  - Notosolenus sp.

TABLE II. (Continued)

Mastigophara (flagellates) (con't)
- Oicomonas socialis
- Peranema trichophora
- Tetramitus sp.
- Trepmonas agilis
- "Many small flagellates"

Infusoria (Ciliates)
- Amphileptus sp.
- Amphisia sp.
- Aspidisca sp.
- Blepharisma sp.
- Carchesium sp.
- Chilodon sp.
  - cucullus
- Cinecochilum margaritaceum
- Colpidium sp.
  - striatum
- Colpoda sp.
  - inflata
- Cyclidium sp.
  - glaucoma
- Euplotes sp.
  - sharon
- Glaucoma sp.
  - scintilans
- Halteria sp.
- Holophrya sp.
- Lembus sp.
- Lionotopsis sp.
- Lionotus sp.
  - fascicola
- Loxodes sp.
- Loxophyllum sp.
- Macrymaria sp.
- Metopus sp.
- Microthorax sp.
- Nassula sp.
- Opercularia sp.
- Oxytrichia sp.
  - pellionella
- Paramoecium sp.
  - caudatum
- Pleuronema sp.
  - chrysalis
- Pleurotricha lanceolata
- Podophrya sp.
- Prorodon sp.
  - teres
- Spirostonum sp.
- Stentor sp.
- Stylonichia sp.
  - pustulata
- Uroleptus sp.
- Uronema sp.
  - marina
- Vorticella sp.

Metazoa
- Turbellaria (Flat Worms)
  - Stenostomum leucopus
- Rotatoria (Rotifers)
  - Euchlanis dilatata
  - Philodina roseola
  - Rotifer vulgaris
- Nematoda (Nematode Worms)
  - Diplogaster strictus
  - Diploscapter coronata
  - Dorylaimus saprophilus
  - Rhabdites sp.
- Gastrotricha (Gastrotrich Worms)
  - Chaetonotus sp.
- Oligochaeta (Round Worms)
  - Aeolosoma hemprichi
  - Dero limosa
  - Limnodrilus sp.
  - Lumbricillus lineatus
  - Lumbricus rubellus

TABLE II. (Continued)

Oligochaeta (Round Worms) (con't)
- Pristina sp.
  - longiseta
- Tubifex sp.

Polychaeta (Polychaete Worms)
- Polychaeta sp.

Crustacea
- Cyclops sp.

Mollusca
- Lymnaea humilis modicella
- Physa anatina
  - cubensis
  - halei
  - integra

Tartigrada
- Macrobiotus sp.

Arachnida
- Torrenticula anomala

Insecta
- Cercyon fimbriatus
- Diploneura cornuta
- Leptocera fontinalis
- Limonia simulans concinna
- Psychoda alternata
- Scatella paludum
  - stagnalis

sp., *L. fascicola, Euplotes charon, Cyclidium glaucoma, Pleurotricha lanceolata, Oxytricha pellionella* and *Uronema marina, U.* sp., *Vorticella* sp., and *Pleuronema chrysalis;* Rare: *Colpidium striatum, Glaucoma scintillans, Prorodon teres, Stylonychia pustulata, Podophrya* sp., *Paramoecium caudatum,* and *Opercularia berberina;* Metazoa: *Turbellaria* (flat worms): *Stenostomum leucopus;* Rotatoria: *Euchlanis dilatata, Philodina roseola,* and *Rotifer vulgaris;* Gastrotricha: *Chaetonotus* sp.; Nematoda: unidentified; Annelida: *Aelosoma hemprichi.*

In certain areas, populations of snails can develop in trickling filters. Ingram *et al.* have reported (1958) that at least five species of snails have been found in the United States on trickling filters. *Physa anatina* was found at Urbana-Champaign, Illinois, *Physa halei* at Fort Worth, Texas, *P. cubensis* at Gainesville, Florida, and *P. integra* at Dayton and Hillsboro, Ohio. In addition, *Lymnaea humilis modicella* was found once in low numbers at Urbana-Champaign. Serious damage to equipment was reported as a result of the activities of *P. integra* at Dayton, and of *P. cubensis* at Gainesville.

It is not to be assumed that all organisms presented in the accompanying composite list (Table II) are present on all trickling filters at the same time. Many of them occur in very low numbers indicating that they are transitory rather than members of the population at the time of sampling. Others are very abundant. When Hesseltine (1953) studied the trickling filters at Pearl River,

New York, he found that *Fusarium aquaeductuum, Geotrichum candidum,* and *Subbaromyces splendens* were common enough to be considered members of the population, and that other species of molds which were present were considered chance contaminants. Becker and Shaw (1955) scraped surface stone of trickling filters at Pullman, Washington, and Moscow, Idaho, and found so few fungi that they decided fungi were not part of the permanent population although *Fusarium aquaeductuum* was present at times in large enough amounts to produce orange colored patches on the filters. Fungi isolated from filter effluents indicated a certain amount of activity on the filters but the extent of this activity can only be guessed on the basis of work done on other filter populations.

Rate of Population Development

Before a complete description of the biota of the trickling filter can be given, information should be available on the development of the population. A method of sampling the algal and fungal components of the population during its developmental and mature stages has been described (Cooke 1958; Cooke and Hirsch 1958). Briefly the technique includes exposure of weighed glass slides on the filter stone, removal of the slides at weekly intervals, and study of the populations developed there. The study is accomplished quantitatively by weighing air-dried materials on the slides, by reviving some members of the population, plating them and counting the colonies or by directly counting cells and cell clusters in the materials which have been resuspended in water.

At the Dayton, Ohio, sewage treatment plant, studies were made simultaneously on a low-rate and a high-rate trickling filter. Sixty sets of frames, each with four attached slides, were placed on each filter. Slides were returned to the laboratory at weekly intervals for 57 weeks. Colony counts of fungi found in the rewet material were obtained for each slide from each filter. These are presented in Table III for the first 25 weeks for both filters. A mathematical curve, the logistic, was fitted to the population growth data, that is, colony counts from the start of observation to the time at which these counts appeared to level off. The equation for this curve is:

$$\text{Expected } y_t = -\frac{k}{1 + e^{\alpha + \beta \log t}} = k \frac{e^{\alpha + \beta \log t}}{1 + e^{\alpha + \beta \log t}}$$

where y_t is the colony count at time t, measured in weeks, k is the plateau level, determined as the average of the first several colony counts (7 for the low-rate, 4 for the high-rate) after what appeared to be the leveling off time (15 weeks for the low-rate, 19 for the high-rate filter), and α

TABLE III. Fungal species and colonies on exposed slides (first 25 weeks)

Date of Harvest	Week	Number Days Exposure	Low-Rate Filter			High-Rate Filter		
			Number of Species	Number of Colonies	Air dry Weight (gm)	Number of Species	Number of Colonies	Air dry Weight (gm)
11-29	1	7				10	1,662	0.33
12-6	2	14	12	42	0.06	19	989	0.41
12-13	3	21	12	41	0.09	19	740	0.74
12-20	4	28	9	3,190	0.16	17	47,002	0.96
12-27	5	35	12	1,845	0.21	21	48,657	1.40
1-3	6	42	17	35,525	0.39	25	56,694	1.43
1-10	7	49	23	40,463	0.59	23	70,100	1.65
1-17	8	56	19	79,365	0.38	18	174,125	1.35
1-24	9	63	16	124,157	0.81	16	202,025	1.42
1-31	10	70	15	7,696,770	0.88	17	168,175	1.61
2-7	11	77	18	451,675	0.75	23	320,250	0.53
2-14	12	84	22	369,475	0.58	26	344,800	0.69
2-21	13	91	20	564,130	0.64	25	321,055	0.93
2-28	14	98	15	1,988,130	0.78	19	1,473,675	0.64
3-7	15	105	16	2,030,975	0.99	19	832,975	1.43
3-14	16	112	18	16,439,000	1.14	14	3,136,750	1.51
3-21	17	119	14	9,929,750	0.88	16	1,112,400	0.71
3-28	18	126	14	2,731,250	1.78	15	1,654,750	1.05
4-4	19	133	12	9,077,050	0.59	15	6,814,750	1.40
4-11	20	140	14	13,872,000	1.06	18	14,131,250	1.82
4-18	21	147	12	7,161,750	0.87	12	10,921,000	1.75
4-25	22	154	13	5,114,750	0.57	16	13,413,250	2.20
5-2	23	161	12	10,610,000	0.69	15	7,200,000	1.76
5-9	24	168	13	2,730,000	1.10	15	5,575,000	1.78
5-16	25	175	12	13,495,000	1.28	17	7,935,000	1.50

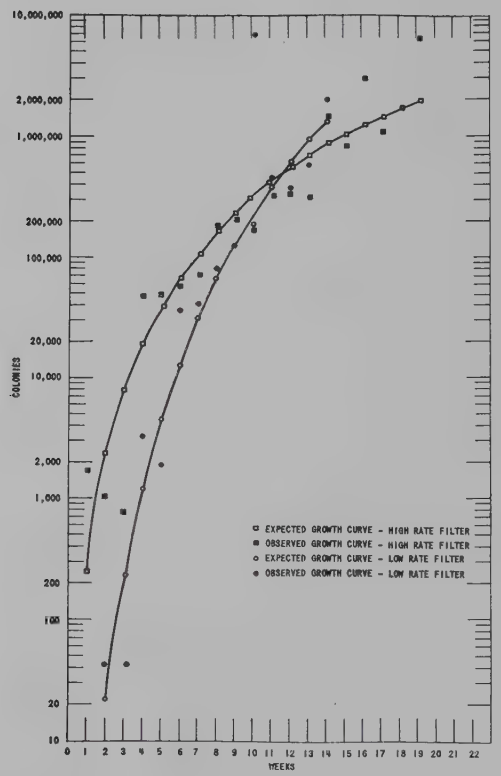
COLONIES
WEEKS
EXPECTED GROWTH CURVE - HIGH RATE FILTER
OBSERVED GROWTH CURVE - HIGH RATE FILTER
EXPECTED GROWTH CURVE - LOW RATE FILTER
OBSERVED GROWTH CURVE - LOW RATE FILTER

FIG. 1. Colony counts observed and expected under fitted logistic curve.

and β are parameters (Fig. 1). For the high-rate filter, k was found to be 12,800,000, and for the low-rate filter, k was 9,200,000.

Estimates of the parameters α and β are obtained by putting the above equation in the following linear form in terms of common logarithms:

$$\text{Observed } \log_{10} \frac{y_t}{k - y_t} = .43429 \ (\alpha + \beta \log t).$$

To ease the calculations, the factors $y_t/k - y$ were multiplied by 100,000 in the case of the high-rate filter and by one million for the low-rate filter.

Thus, if $\frac{y_t}{k - y_t} := 100{,}000 \ \frac{y_t}{k - y_t}$, we obtain

$$\log_{10} \frac{y_t}{k - y_t} := 5 + .43429 \, \alpha + .43429 \, \beta \log t$$

(in the case of one million, the 5 on the right-hand side is replaced by 6). Thus, plotting the observed numbers on the left-hand-side versus log t, a good straight line was obtained on log-log paper whose intercept, say A, equal to 5 + .43429 and whose slope, B, equal to .43429, were estimated by the usual least squares techniques. Then it was estimated that

$$\alpha = \frac{A - 5}{.43429} = 2.30259 \ (A - 5), \text{ and } \beta = \frac{B}{.43429} = 2.30259B$$

For the low-rate filter these estimates were $\alpha = -16.92$, $\beta = 13.25$, and for the high-rate filter $\alpha = -10.87$, $\beta = 7.19$.

Using these values of α and β and the previously mentioned values of k, Figure 1 plots these values on semi-log paper for each filter and shows the observed colony counts and those expected under the fitted logistic curve.

It will be noted that the population growth curve rises more sharply and steeply on the low-rate than on the high-rate filter and would arrive at the upper asymptote, k, more quickly. In view of the fluctuations observed during later weeks, it is believed that there is, in the long run, no real difference between the two selected values of k. The logistic appears to be an adequate representation of the increase in the number of colonies during the build-up phase.

Description of the Biota

The community of organisms occupying a trickling filter, and the changes through which it goes as it develops from its inception or as a result of changes in dosing or in quality of applied sewage, can be described in terms of the formulae given by Major (1951). His basic formula can be modified for application to this type of population as follows:

$$b = f_b \ (cl, p, r, o, t)$$

where b, the biota of a specific trickling filter, is a function of cl, the regional climate, p, the physical and chemical quality of the applied sewage at time zero, r, the fixed operational conditions of the specific filter, o, the biotic effect of the organisms of the community and of man, and t, the time.

At any moment in time the biota of the filter becomes adapted to conditions of growth on the filter through natural selection rather than deliberate seeding of special segments of the population. The most important parts of this equation are thus p and o. The kind of sewage p applied to a filter will determine the members of the population, since some species will not be able to tolerate some of the sewage materials because of toxicity or inability to use them as food. The factor of man's interference o_h with the population

is important since dosing rates may vary, different types of sewage may be applied at different times, and other operational problems may interfere with one or another type of population. Factors of regional climate *cl* will be relatively constant within one filter although they may vary between different parts of the country or between different types of filter. Within one filter, or one filter field, the regional climate will not vary and will not be particularly important except to the immediate surface layer. Within one filter, temperature of applied sewage will be relatively constant and will be affected only slightly by air temperature. Precipitation in the form of applied sewage will be constant except during periods of heavy rainfall when some of this water is diverted to the filters and is received in the form of more dilute sewage applied more rapidly than usual. Effects of such dilution are usually of brief duration and not of catastrophic importance. Some sloughing may result but recovery is relatively rapid. Effects of the *r* type would be noticed on the filter by the differing populations on the surface layer of stone, because of the presence of light-sensitive algae and fungi, as contrasted with those populations at lower levels. Types of filter construction, ability to prevent ponding, and rate of application of sewage so far as diameter of distributor arms and stationary nozzles are concerned, would be noted in variations of *r*-type effects. Effects of time *t* would vary only slightly if the sewage dosage throughout the year were relatively constant in composition and rate of application, and if the sewage were applied to a well designed and constructed filter. That is, throughout the year, one could expect a certain type of biota to develop on a trickling filter under relatively constant conditions of regional climate, including normal seasonal fluctuations, relatively uniform municipal or industrial waste applications, relatively uniform and continuous operation of the filter, and relatively uniform development of the population, including growth, death and replacement of component parts, without undue interference from man.

Variations in populations occur when dosing rates are changed, type of sewage applied is altered chemically or physically, filters are stopped for servicing, flooding conditions are induced by excessive precipitation or in attempted control of insect or snail populations, or when other factors are altered. Changes in population patterns can be noted by casual macroscopic observation when excessive sloughing occurs, but such observations are not useful unless accompanied by detailed analyses of all aspects of sewage influents and effluents and of engineering factors involved.

Activities of Segments of Filter Bed Populations

It has been suggested, in connection with the listing of the several groups of organisms, that during the course of their life on or in the microbial film these organisms contribute to sewage purification. Upon and within each filter bed a balanced population develops. The population of the film is built up gradually, although the time required may be as short as 50 days (Gilcreas and Sanderson 1940). Its members are derived from various sources and received by the filter either from influent sewage, from initial seeding by the use of effluents from other trickling filters, or by settling of disseminules from the air upon the filter. Such members of the raw sewage population as are readily adapted to life on the filter settle out and become attached to the filter stone. If they can successfully compete with the population already present they will become members of the population of the microbial film.

The algae derive some mineral and nitrogen nutrition from the sewage and are close to an ample supply of carbon dioxide. In turn, they add oxygen to the water in which they are continually bathed. Bacteria and fungi are able to remove quantities of solid, colloidal, and dissolved organic materials from the water through metabolism and by supplying a film onto which many of these materials can be adsorbed and thus effectively removed as the sewage passes through the filter. Protozoans and smaller metazoans easily devour large numbers of bacteria, thus removing members of that population and making space in that particular ecological niche for additional bacteria. This activity tends to control bacterial multiplication keeping it in a continual logarithmic growth phase. If the organism has a large enough "mouth," yeast cells may also be ingested and a similar control is effected on the yeast population. The larger metazoa, such as annelid worms, insect larvae, and snails, browse on the larger fungal and algal populations. Although they are not necessarily carnivorous, the metazoa may ingest, at the same time, any of the smaller organisms and sludge materials adsorbed upon the biological film on which the larger metazoans are feeding.

The concluding statement by Ingram *et al.* (1958) may be elaborated as follows: In removing organic slimes through feeding, snails and annelids remove some percentage of B.O.D., as do various insect larvae. They can thus be looked upon as "crawling B.O.D. removed," as *Psychoda* and other flies and insects may be visualized as representing "flying B.O.D. removed." While the efficiency of this removal has never been evaluated satisfactorily, it is indicated by the large numbers of filter flies around trickling filter installations,

and by the snails, as many as a ton, that can be removed from a trickling filter plant in a day. In terms of food chains, annelid worms, insect larvae, and snails represent the terminus of production on the trickling filter.

Using chemical and biological analyses of materials on a new trickling filter in New York State, Gilcreas and Sanderson (1940) were able to determine that there was a gradual increase in the degree of oxidation of organic and nitrogenous matter in settled domestic sewage at the temperatures received coincident with the gradual development of microbial populations. As a result of a study conducted during the first 107 days of operation it was found that complete oxidation of nitrogenous compounds was effected after 40 days, 50 days were required for total development of the characteristic biota of trickling filters, and 60 days were required for maximum reduction of carbonaceous organic matter.

C. E. Renn (1956) stated: "I am inclined to prefer Dr. Phelps' view of the role of the trickling filter to the more conventional conception of high oxidation rates on surfaces. We have no comparable experience with other types of surfaces that justifies the extraordinarily high rates of oxidation that are implied by assuming that the B.O.D. of a waste is removed in the interval of liquid passage. Rather, there is a great deal of evidence to show that we accumulate a large stock of organic material locally, through high rates of adsorption, and that the accumulated organic materials are oxidized at rates comparable to those of other organic systems."

Activities of the Microbial Film

A trickling filter is so designed that a large amount of biological film is exposed to the flow of sewage. Depending on plant design, this liquid material has passed through preaeration and settling tanks, as at Dayton, so that a portion of the solid, colloidal, and dissolved organic materials has been acted upon and settled out before the liquid reaches the filters. However, a considerable amount of dissolved, colloidal, and solid material remains. As the liquid passes over or through the film, some of these materials are removed through metabolic processes if microorganisms and sometimes of macroorganisms, and additional portions are removed by adsorption on the film. The organic nitrogen content is a measure of the decomposable materials present at any time or place and is used together with B.O.D. as an indicator of the purification effected within a process.

Is it possible to relate the extent to which the removal of organic matter and the mineralization of various constituents of sewage materials is effected by the organisms of the microbial film to the numbers and types of organisms on the surfaces of the filters at the Dayton treatment plant?

Some idea of the potentialities of this question may be gained from the fact that a single trickling filter, 165 feet in diameter, 7.5 feet deep, is filled with 160,270 cu. ft. of limestone slag rock of varying sizes, usually 3-5 inches in diameter, length or width. A flat circular surface 165 ft. in diameter comprises an area of 20 million sq. cm. The upper surface of the stone on a trickling filter is even more extensive because of the irregularities of the stone. The sampling technique included 75 sq. cm. of glass slides on which determinations were made at weekly intervals. Such sampling took into consideration only the initial contact of the sewage with the microorganisms and did not consider the subsequent flow of sewage through a 7.5 foot column of rock. Levine (1938) has shown that as sewage passes downward through the filter the nature of the materials in it become progressively different resulting in gradual downward change in the biota acting upon it.

Preaeration tanks were placed in service at the plant in July 1954, but the complete effect of this type of early stage treatment, preceding primary settling, was not felt on the filters until the following May. This delay may have resulted from the further complication that the filter beds were temporarily by-passed, because of repair shutdowns for three periods between January and April. Throughout the study periods, the high-rate filters took a maximum load of sewage while the low-rate filters received only the excess. Materials entering any of either type of filter were not metered, nor is there a record of the hours or of days during which the low-rate filters were not operating. Low-load periods occurred on weekends and during the night. Since effluents from the two types of filters were not kept separate, data for filtered sewage represent a composite from both types. On the other hand, only data from the slides exposed to the surface of a high-rate filter are used in comparing results obtained on analysis of filtered sewage composited from both filters. On the basis of such data, and because only the surface of the beds was sampled, it may be surprising to find any correlation between air-dry weight of organisms and amount of activity produced by such organisms.

Using available climatic and plant records (Fig. 2), an attempt was made to determine whether the average weekly air temperature (Vandalia, Ohio), the average monthly sewage temperature, and the total weekly precipitation (sum of the higher of the two daily recordings from Vandalia

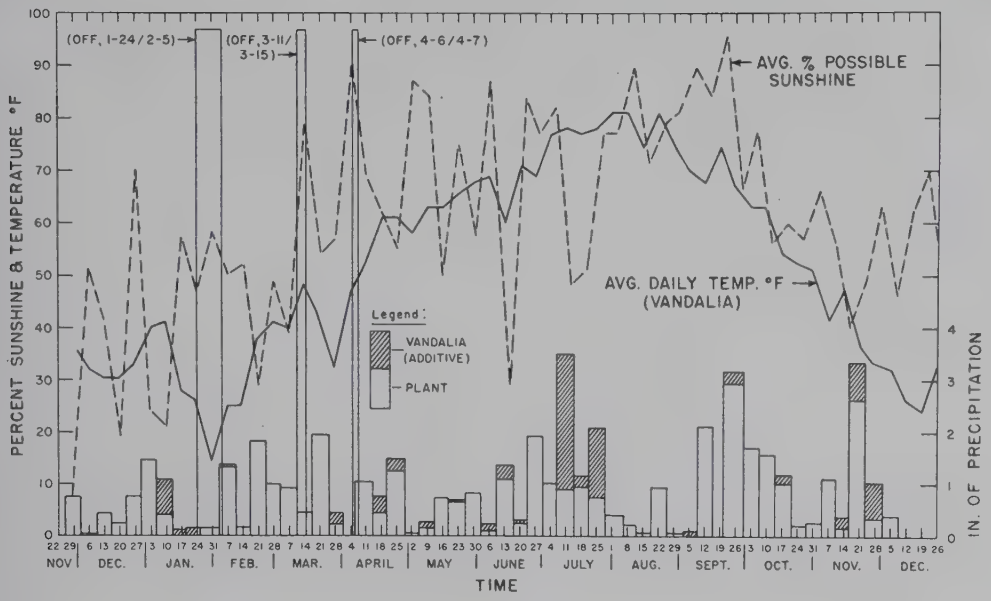

FIG. 2. Weekly averages of average daily temperature, average percentage possible sunshine, and total effective precipitation for the Dayton area.

and the sewage treatment plant) showed correlation with the amount of growth on the slides as indicated by average weights of material on four slides from each of the high- and low-rate filters.

Weight per slide.—Certain discontinuities in the growth curve were traced to periods when the plant was shut down, or the filters by-passed Enough time was subtracted from those periods associated with readings following shut-downs to make the weight on the slides immediately following the shut-down coincide with the weight of the original build-up preceding the shut-down. It was found that growth following a shut-down was noticeably slower than that preceding a shut-down when the same weight of material occurred on the slides (Fig. 3). Straight-line curves fitted to the data on log-log paper show that the percentage growth rate is inversely proportional to time. Growth during the first month of exposure (before the first shut-down) was about 61 mg. per 30 days, but after the shut-downs, the growth rate was only 35 mg. per 30 days when the same weight (25 mg.) of organisms occurred on the slides. On this basis, an equilibrium had not been reached at the end of the exposure period since the growth rate was 17 mg. per 30 days during the 12th to 13th month.

Average weekly air temperature (at Vandalia).—A trigonometric sine function was fitted (Fig. 4) to these data successfully. The minimum (trough) value of the fitted curve is 28.2°F. and occurred in the 10th week of the experiment

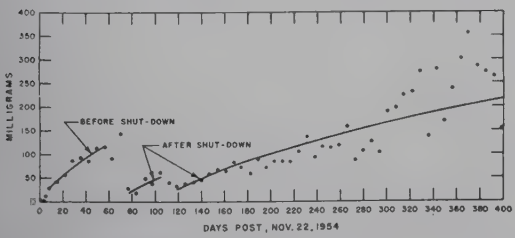

FIG. 3. Cumulative growth on frames showing influence of shut-downs and rate of development.

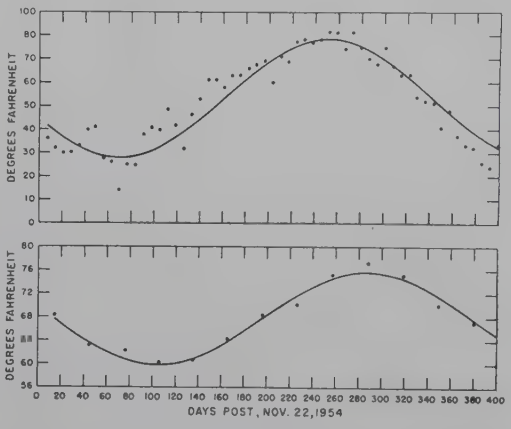

FIG. 4. Average weekly air temperature (Vandalia, Ohio) and average monthly temperature of raw sewage (Dayton).

(ending Jan. 31, 1955). The maximum (peak) value of 78.2°F. occurred six months later in the 36th week (ending Aug. 1, 1955). The rise from the trough to the peak is a mirror image of the drop from the peak to the next year's trough.

Average monthly raw sewage temperature.—A sine curve (Fig. 4) also fitted these data well. The minimum of 59.7°F. lay in Feb. 1955, and the maximum of 75.6°F. lay in Aug. 1955. The sewage temperature curve lagged the air temperature curve by about 40 days, but since the sewage temperatures were monthly averages and air temperatures were weekly averages, the lag could have been as little as three weeks.

Total weekly precipitation (sum of the higher of two daily recordings).—(Fig. 2) There was no trend in the average weekly precipitation during the year. Weekly precipitation apparently varies at random an average of 0.90 inches per week, but is not symmetrically distributed about this average. That is, there were more values below the average (35) than above (22).

Correlations.—Several statistical techniques were tried to determine whether or not the microbial film was affected by the climatic conditions to which it was subjected throughout the year. No evidence exists to indicate a relationship between the irregularities (sloughing or unusually rapid growth) in slide weights and corresponding deviations from seasonal patterns of the weekly average air temperature, raw sewage temperature, or total weekly precipitation figures.

Chemical and physical analyses of sewage.—A chemical and physical check is maintained by the chemical laboratory of the Dayton sewage treatment plant on the effectivity of the treatment. At four stages in the treatment process—raw, settled filtered and final—the B.O.D., dissolved nitrogen, ammonia nitrogen, organic nitrogen (Fig. 5, expressed as percent removal), chlorides, and suspended solids (Fig. 6) are analyzed. The 5-day B.O.D. and suspended solids are measured daily at each of these points. The other values are taken on the 1st, 8th, 15th, 22nd, and 29th of each month unless one of these dates happens to fall on or near a holiday. On the accompanying graphs, values for these factors are plotted as near the day on which sampling was done for the week as possible. Values used in the present study include only those for settled sewage entering the filters through the distributor nozzles, and filtered sewage, as it leaves the filters before it reaches the final settling basin.

Correlations.—Of the five chemical factors measured in the settled sewage, only the B.O.D. was related to variations in the growth rate of organisms occurring in the slimes with any degree of significance, and even the B.O.D. fails to explain any but an insignificant portion of the variability in the growth pattern of the organisms on the surface of the filter. Most of the statistical analyses of the effect of the chemicals on growth

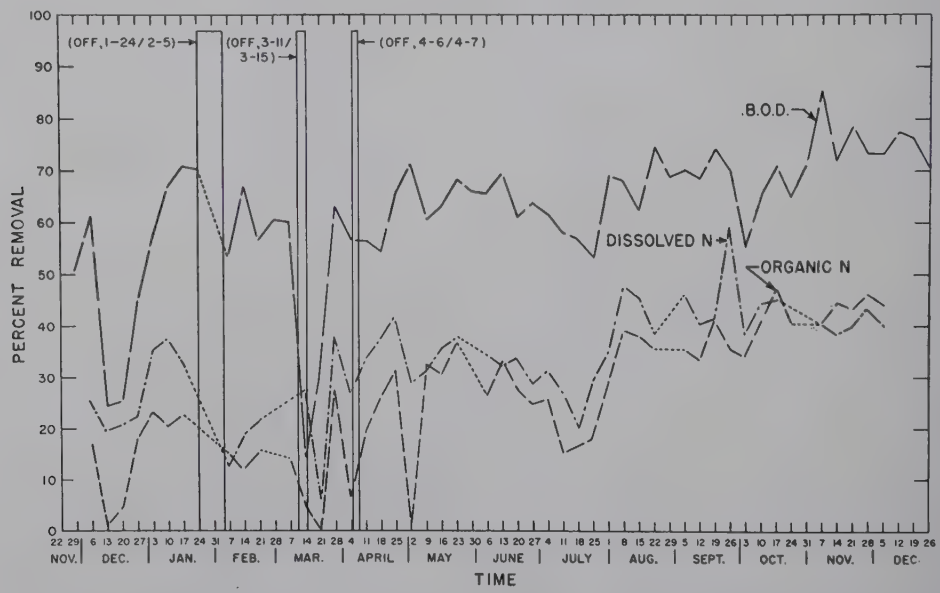

FIG. 5. Percentage removal of B.O.D., dissolved nitrogen and organic nitrogen during filtration.

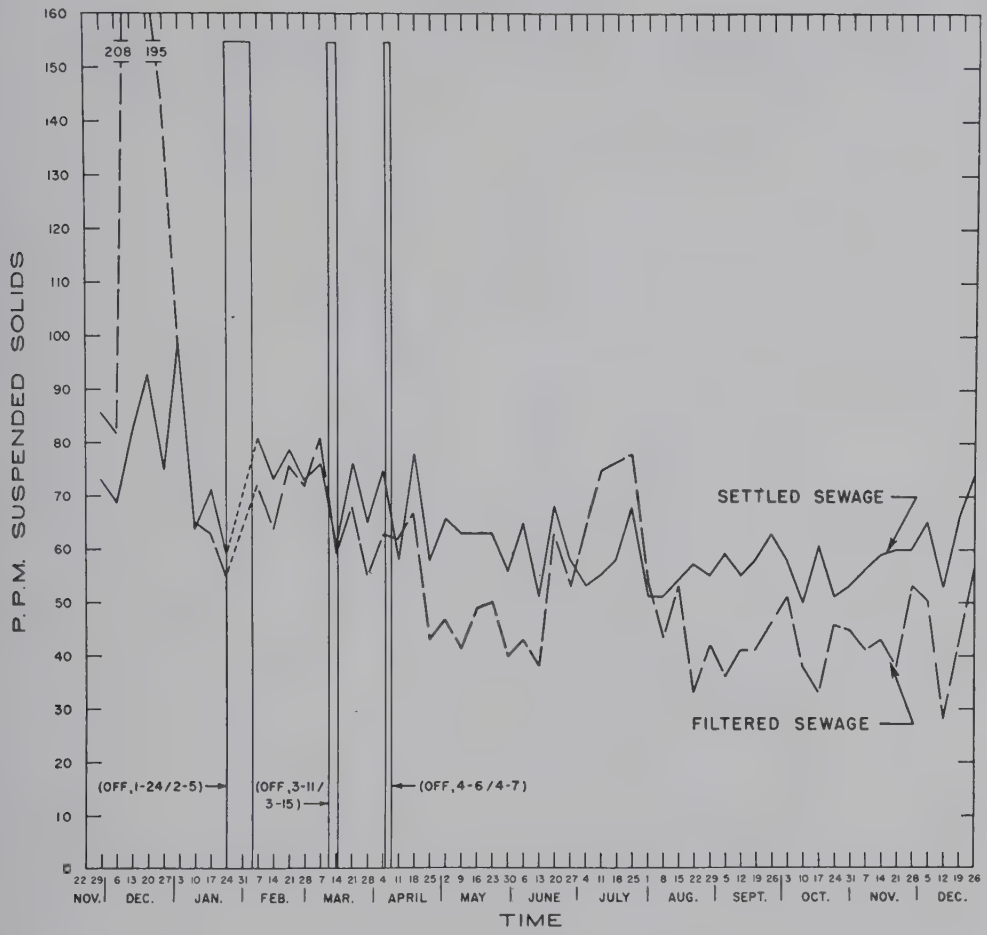

FIG. 6. Suspended solids in settled and filtered sewage.

of microorganisms and of the organisms on the chemicals were made with the use of regression coefficients. No significant regression coefficients of slide weights themselves were noted on the chemicals in the settled sewage.

Regression coefficients were found to be satisfactory for assessing the possible dependence of the chemical concentrations in the filtered sewage on the weight of organisms on the slide surfaces. Using this technique it was found that the differences between the B.O.D., organic nitrogen, and dissolved nitrogen in settled and in filtered sewage were related to slide weights. Thus these differences can be postulated as attributable to the removal from sewage of materials, adsorbed or as increased growth, added to the weight of organisms present. Such slide weights represent neither increment nor total accumulated growth but material present at any one date following addition by growth and adsorption, as well as loss by death and sloughing. On the other hand, the amounts of ammonia nitrogen and suspended solids in either the settled or filtered sewage did not appear related in any way to the organisms on the surface of the filter. In the case of suspended solids, this observation is of interest since a good proportion of these solids is composed of sloughing from the microbial film.

Adaptation to Habitat

The organisms which live in the sewage treatment plant, especially those on the trickling filters, have become adapted to life in a waterfall-cascade system in which the effluent from primary settling tanks is the liquid passing over the rocks. This liquid contains a quantity of suspended, colloidal, and dissolved materials, primarily waste materials resulting from human metabolism but also includ-

ing such wastes as laundry and wash water, industrial wastes, soil run-off, and wastes from garbage disposal units. Fundamentally, there is little difference between a habitat in which such materials are present and a soil habitat which contains fragments of dead plant or animal parts, as well as the excrement of various native animals. Many, if not all organisms which live on trickling filters have become adapted to this condition of existence following the development of a capacity to live all their lives in the presence of water.

According to various interpretations of the Kolkwitz and Marsson (1911, 1950) system of classification of zones of pollution in streams (Whipple, Fair and Whipple 1947), the solids removed from sewage during the settling process and treated in sludge disgesters form a *polysaprobic* habitat while the settled liquid passing over the trickling filter provides a habitat interpreted as *α-mesosaprobic*. Thus all of the organisms found living in a trickling filter (Table II) could be interpreted as *α-mesosaprobes*. However, there appear to be different degrees of adaptation to such an environment. Cooke (1957a, 1957b) has indicated that for the fungi there may be four different types of response to the pollutional habitat. The terminology defined in these papers is not necessarily restricted to fungi but may be applied to all organisms living in the habitat. Those species which have never been reported except from trickling filters, dung, decaying animal bodies under water, and similar habitats may be considered *lymabionts*. At least three species of fungi (*Pilobolus* sp., *Ascodesmis microscopicum*, and *Subbaromyces splendens*), *Tubifex* worms, and possibly some bacteria and protozoans may be included in this category.

Most of the organisms found on trickling filters may be considered as *lymaphiles*. They are closely associated with this type of habitat although in certain instances they may be found in other habitats where decay occurs or where conditions are tolerable.

Of the fungi, at least, a large number of species, represented by a small number of individuals, are considered to be *lymaxenes*. These organisms are well adapted to living in habitats other than those which may be considered sewage polluted, but for short periods of time they can join the other members of the trickling filter population. At such times they may be passing through the plant as chance contaminants and become trapped in the slime by adsorption or by mechanical screening methods.

One will never find a *lymaphobe* in this habitat at least in vegetative condition. Such a find would be the result of a chance contamination, a spore being carried through the plant by the water in which it was accidentally picked up.

While much of the biology of algae, protozoans, metazoans, and bacteria which are found on the filters as members of the population is not well known, it may be assumed that these organisms, too, will be found to fall into the biological classes listed above. Trickling filters, as such, have been in existence for hardly 80 years (Stanbridge 1954), and it does not seem likely that a whole new population of organisms could have developed during that time. It seems more probable that members of other populations have become adapted during this period of time to life in this specialized habitat. Prior to the formal recognition of the need for sewage purification in the late nineteenth century, sewage disposal or removal was a more or less individual matter and where sewer lines existed they only carried the wastes to the nearest streams. Certain members of the population of organisms adapted to a sewage habitat may have originated from the biota of such waste-carrying channels.

The Ecosystem

The ecosystem of the trickling filters may be summarized by the chart presented in Figure 7. This has been adapted from Clarke (1954) whose original chart (p. 467) has been modified to describe the specialized ecosystem under consideration. In this chart it is assumed that the trickling filter whose population is being described is not covered and that direct sunlight is being supplied to the algae which are the only green plants functioning in the treatment of sewage. It is indicated that the sewage being applied is an essential component since the population is developed for the treatment of this material. A somewhat artificial pair of categories has been introduced by the splitting of "decomposers" into primary decomposers, those which act directly on the sewage components, and secondary decomposers, those which act on dead tissue formed through development of the biological film.

From sewage, green plants can obtain certain required mineral supplies as well as nitrogen and phosphorus so that in the presence of light growth can be effected. It is possible that within the microenvironment there is present a larger amount of carbon dioxide than in many habitats because of the great numbers of microorganisms existing in an actively metabolizing state. Those green algae which occur on the filter, then, are probably conditioned to a slightly higher percentage of atmospheric carbon dioxide than other algae or than

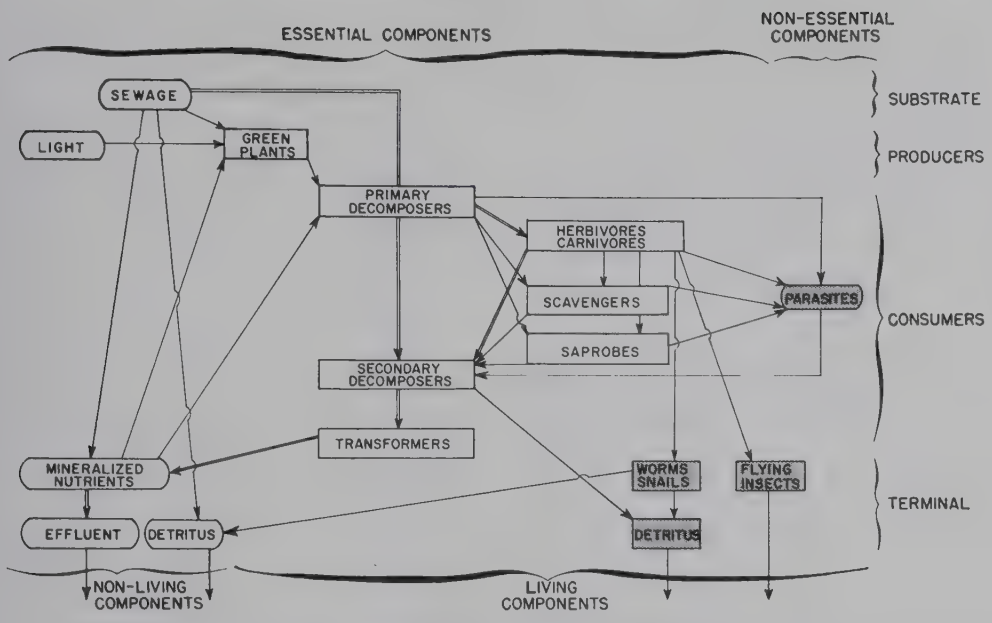

FIG. 7. Principal steps and components in the trickling filter ecosystem.

algae of the same species in a different aquatic habitat.

In some cases it is difficult to define the exact meaning of the terms herbivores and carnivores as related to the organisms on the filters, because of the problem of separating plants and animals in a population of this type. In some cases, pigmented cells, unpigmented cells and nonliving particulate matter all form the basis of the food supply of grazing and scouring organisms.

Herbivores and carnivores include protozoans and metazoans which feed only in part on bacteria. These organisms thus exercise a control on the rate of growth of the film and on the amount of growth which may be present. *Colpidium* and other ciliates keep the bacterial populations in a continuing state of growth by ingesting bacterial cells and permitting the continued rejuvenation of that segment of the biota. In addition, other protozoans may act in a similar way and larger animals, such as rotifers, may ingest larger unicellular organisms including algae and yeasts with similar effects. Insect larvae, sludge worms and snails graze on the film. These organisms are probably both carnivores and herbivores since they may ingest both pigmented and unpigmented cells, bacteria, fungi, algae and protozoans. Adsorbed on the less motile components of the film are sludge deposits of various types which may be ingested together with the film so that in a sense these browsing and grazing organisms are scavengers and saprobes as well.

It is possible that some members of the population are parasitized by some microorganisms. Such relationships have not been shown directly, but in the examination of algal material submitted to him for identification Drouet (in Cooke and Hirsch 1958) indicated that *Pleurocapsa*-like material could have been a parasitized form of an *Anacystis*-like species. *Characium* sp. was found growing attached to *Stigeoclonium nanum* but this was probably an epiphytic relationship. While a number of types of bacteria and fungi are known to be able to attack members of the trickling filter biota in other habitats, parasitic relationships between the members of this biota and each other or additional invaders have not been observed. Rather, a mutualistic relationship has been established especially between the unicellular colonial organisms and the filamentous organisms in which the byproducts of the metabolism of one type of species are removed by another thus reducing potential toxic effects.

Scavengers and saprobes may degrade the dead tissues of the primary decomposers as well as components of the sewage but in turn they are subject to decomposition by the secondary decomposers whose byproducts are transformed into

mineral nutrients which may also be added to the influent sewage to help restart the cycle.

Summary and Conclusions

The trickling filter is an ecological tool of the sanitary engineer in the treatment and purification of domestic sewage and industrial wastes and terminology developed in its use is described. The biota of trickling filter slime has received little attention as a working population unit although various segments of that unit have been described.

The populations of several trickling filters in the United States and England are reviewed according to limited studies based on either bacteria, fungi, algae, protozoans, worms, insects or snails. An integrated list is presented to indicate something of the complexity of the biota.

A series of slide exposure samples of trickling filter biota has been studied with special reference to algae and fungi. As a result of fungal colony counts made from revived growths, a logistic curve has been developed to describe the rate of development of the population. The more rapid and steeper rise of the curve on a low-rate than on a high-rate filter is more apparent than real since the same curve is obtained in plotting the lower values of the two curves in parallel, so that no actual difference was noted between the two types of filter.

The functional, factorial description of a community can be used to describe the biota of a trickling filter. Climate is relatively uniform for a single filter except in periods of excessive precipitation or run-off. The biotic effects within the community are limited to replacement phenomena should an organism be unable to meet competition, and to the fact that grazing organisms tend to control the rate of population growth. Operational conditions of a specific filter, man's effect on a filter as operator and controller of the process, and the physicochemical nature of the applied sewage would be effective in time, but at the end of a study of samples accumulative up to one year the effect of time itself had not been completely discovered.

Filter bed populations are effective in removing a large percentage of solid, colloidal, and dissolved matter in settled sewage, thus reducing the B.O.D. of that sewage. This removal is not by metabolic processes alone but by adsorption on the film as well.

Growth on the stones of the filter develops rapidly at first but slows down as the film matures. In the case of reported experiments, points at which such slowing was most noticeable coincided with periods during which the filters were shut down for repair. No correlation between surface growth rate and total weekly precipitation, average weekly air temperature, and average monthly sewage temperature was noted. Surface growth was not correlated with differences between settled and filtered sewage of ammonia nitrogen, organic nitrogen, chlorides or suspended solids. However, a slight correlation was noted in the case of B.O.D. removal.

As a whole, the habitat is α-mesosaprobic. However, different component organisms vary in their ability to tolerate the conditions to which they are exposed. Species represented most abundantly are lymaphiles. Many species represented by few individuals are lymaxenes, while the lymabionts have not yet been noted elsewhere. Lymaphobes are not expected in this habitat although an occasional spore or resting body may be observed.

The total ecosystem includes a few photosynthetic algae but mostly organisms dependent on preformed organic matter. Primary decomposers use such materials as food supplies, may be acted on by herbivores or carnivores or may be parasitized. At death all organisms of the system may be attacked by scavengers or saprobes which act as secondary decomposers whose products are transformed into mineralized nutrients which may reenter the metabolic system.

Acknowledgments

Assistance in laboratory studies has been given by George Matsuura. In statistical analyses, Kenneth A. Busch and Eugene K. Harris gave much help. P. W. Kabler, Ernest C. Tsivoglou, William M. Ingram, Archie E. Becher, and Graham Walton of the Sanitary Engineering Center helped in clarification of sections of the paper. George C. Clarke, Harvard University, kindly criticized the development of the ecosystem and aided in the clarification of the ecosystem chart. R. F. Daubenmire, The State College of Washington, also contributed to clarification of certain passages.

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MONTHLY VARIATIONS OF CARBOHYDRATES AND NITROGEN IN ROOTS OF SANDHILL OAKS AND WIREGRASS[1]

F. W. Woods, H. C. Harris, and R. E. Caldwell[2]

The sandhills of western Florida, now largely occupied by scrub oaks and wiregrass, are capable of growing good stands of pine. Soil moisture is the limiting factor for establishing seedlings in this area, however, and all competing vegetation must be eradicated before pines can be successfully planted or seeded (Woods 1958). An inexpensive method of eradicating the oaks and wiregrass, therefore, would encourage landowners to restore these sites to timber production.

Tops of the oaks and wiregrass are relatively simple and cheap to destroy by fire or mechanical means, but little is accomplished by killing only the tops. Wiregrass generally responds to these treatments with profuse vegetative growth, and oak root collars sprout freely. The amount and intensity of initial sprouting is determined, presumably, by the abundance of reserve food stored in the roots. This study was designed to discover the time of year when carbohydrate and nitrogen root reserves of sandhills scrub oaks and wiregrass are lowest—and hence when these plants can be most efficiently destroyed.

Methods

Turkey oak (*Quercus laevis* Walt.), bluejack oak (*Q. incana* Bartr.), and pineland three-awn (*Aristida stricta* Michx.), commonly called wiregrass, were studied for 3 years.

Two series of sampling points, at locations about 1 mile apart, were established on the Chipola Experimental Forest, in Calhoun County, western Florida. Samples were taken once a month from August through February, and twice a month from March through July. On each date and at each location, two turkey oaks, two bluejack oaks, and two wiregrass plants were chosen at random and sampled. Oak root samples consisted of equal amounts, by volume, of roots of two size classes: 0.26 to 0.50 inch in diameter, and 0.25 inch and less in diameter. The samples for each tree were taken, when possible, from a single lateral root and always from roots in the upper 8 inches of soil. With wiregrass plants, the entire root system was collected. No plant was sampled twice, and no specimens were taken from plants that seemed abnormal or diseased. At each location, samples representing identical species and dates were composited for chemical analysis. Samples from different locations were analyzed separately, and the results averaged.

In the laboratory, the roots were rinsed with cold water to remove soil, cut into short lengths, killed by autoclaving for 5 minutes at 5 pounds of pressure, and oven-dried at 65°C to constant weight. They were then stored in sealed glass jars.

For analysis, the samples were ground to powder. Available carbohydrates were determined by the method of Weinmann (1947) and total nitrogen by the Gunning method (A. O. A. C., 1950) modified to include the nitrogen of nitrates.

Herbarium specimens from each plant sampled were used to describe phenological progression. Reproductive stages were not described because practically all of the trees in the study were too small (10 to 15 feet in height) to bear flowers or fruits.

The soils on the two study areas were classified as Lakeland and Blanton coarse sands, the difference being chiefly in the color of the subsoil. The Blanton soil had slightly more silt and very fine sand (Table I). All other analyses of these two soils were so similar in both locations that it seemed unlikely that soil differences could influence the results of this study.

Carbohydrates in Oak Roots

Carbohydrate reserves in roots of turkey oak dropped rapidly during the spring flush of growth and reached a low point around the first of May (Fig. 1), just when new leaves were reaching full size. The total reserves at this time were approximately half as great as during the dormant season. After this low point, foods accumulated swiftly for about two months and then appeared to trend slightly downward during midsummer. Reserves rose again in the fall, reaching a maximum in November.

Seven vegetative stages could be recognized for turkey oak (Table II). Stages 4 and 5, in which leaves are from half to full size, probably are indicators of low root reserves.

[1] Cooperative contribution of the Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture, and the Florida Agricultural Experiment Station.

[2] Assistant Professor of Silviculture, Duke University, and formerly with the Southern Forest Experiment Station, Marianna, Florida; Agronomist, Florida Agricultural Experiment Station; and Associate Chemist, Florida Agricultural Experiment Station, respectively. Dr. R. W. Bledsoe, Associate Director, Florida Agricultural Experiment Station, took part in the early work.

TABLE I. Analyses of soils from the study areas

Soil type and location	Depth of horizon	Organic matter[1]	pH[2]	Total nitrogen[3]	Moisture equivalent[4]	Mechanical Analysis[5]						
						Very coarse sand	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay
	Inches	Percent		Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Lakeland coarse sand	0–4	2.41	5.45	0.03	2.81	0.8	41.6	40.8	14.9	0.9	0.6	0.4
NW 1/4 of SE 1/4 of Sec. 30, T1N, R1OW Tallahassee Meridian	4–8	.80	5.40	.02	1.08	.8	41.3	39.4	16.1	1.3	1.0	.1
	8–16	.41	5.52	.02	.86	.9	39.9	40.9	15.4	1.5	.9	.5
Blanton coarse sand	0–4	2.30	5.38	.04	2.67	10.7	37.2	31.1	16.2	2.3	2.4	.1
SE 1/4 of SW 1/4 of Sec. 6, T1S, R1OW Tallahassee Meridian	4–8	.94	5.65	.02	1.11	11.0	34.8	30.9	17.9	2.6	2.4	.4
	8–16	.48	5.72	.01	.88	11.8	34.3	28.2	19.4	2.4	3.3	.6

[1]Prince (1955).
[2]Reed and Cummings (1945).
[3]Prince (1945).
[4]Modification of the method of Briggs and McLane (1907).
[5]Bouyoucos (1936).

The seasonal trends of reserve foods in bluejack oak were very similar to those in turkey oak (Fig. 1), but the lowest level came in mid-April. Also, there was no late-summer decrease in carbohydrates, an indication that the late-summer depletion cycle of turkey oak may have been more apparent than real. For bluejack oak, phenological stages 3 through 5 (Table III) seem to be indicators of low root reserves.

Total Nitrogen in Oak Roots

Variations in the yearly cycles of total nitrogen in roots of turkey oak and bluejack oak (Fig. 2) were similar. The major nitrogen depletion cycle corresponded to that of carbohydrates but lasted longer, terminating about the first week in June. The simultaneous depletion of both nitrogen and carbohydrates seems to indicate that they were being used primarily for tissue-building rather than in respiration or other catabolic processes.

Reserve Carbohydrates and Nitrogen in Wiregrass

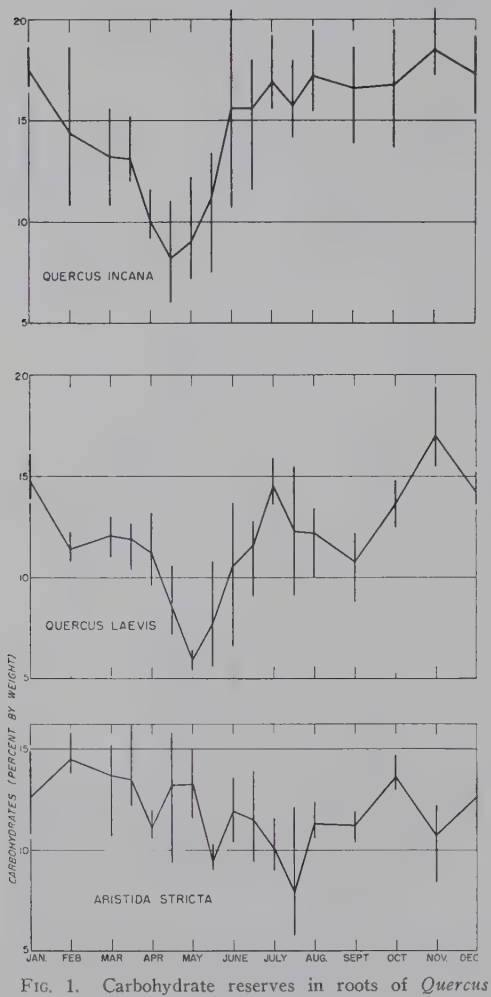
Carbohydrate reserves in wiregrass roots were in least supply during mid-July, and were highest

TABLE II. Vegetative phenological stages of turkey oak (*Quercus laevis*) in Calhoun County, Florida

Stage	Vegetative condition	Approximate time of entry into new stage
1	Bare	January
2	Buds begin to open	Mid-April
3	Small leaves under small (1/16-inch) round fuzzy buds in axils, branches elongating	Mid-April
4	Leaves 1/2 to full size and membranous, axillary tufts of pubescence on lower surfaces of leaves colored light tan, upper surfaces not glossy	Late April
5	Leaves full size and firm, axillary tufts of pubescence on lower surfaces of leaves brown, upper surfaces glossy	Early May
6	Brown spots begin to appear	Mid-July
7	Leaves greenish brown, finally becoming brown	November

TABLE III. Vegetative phenological stages of bluejack oak (*Quercus incana*) in Calhoun County, Florida

Stage	Vegetative condition	Approximate time of entry into new stage
1	Bare	January
2	Buds begin to open	Late February
3	Leaves small with dull upper surfaces and concomitant twig growth	Early April
4	Leaves not yet full size but with glossy upper surfaces, axillary buds small, immature, buff colored	Mid-April
5	Leaves full size, upper surfaces glossy	Early May
6	Small, round buds in leaf axils prominent; scales distinct, a definite brown	Mid-June
7	Leaves becoming brown and spotted	October
8	Leaves brown	December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QUERCUS LAEVIS
ARISTIDA STRICTA
CARBOHYDRATES (PERCENT BY WEIGHT)
JAN. FEB MAR APR MAY JUNE JULY AUG. SEPT OCT. NOV. DEC

FIG. 1. Carbohydrate reserves in roots of *Quercus laevis, Q. incana,* and *Aristida stricta.* Average of 3 years, 1954-1956. Vertical bars through curves indicate range of the 3 annual averages (1954, 1955, 1956).

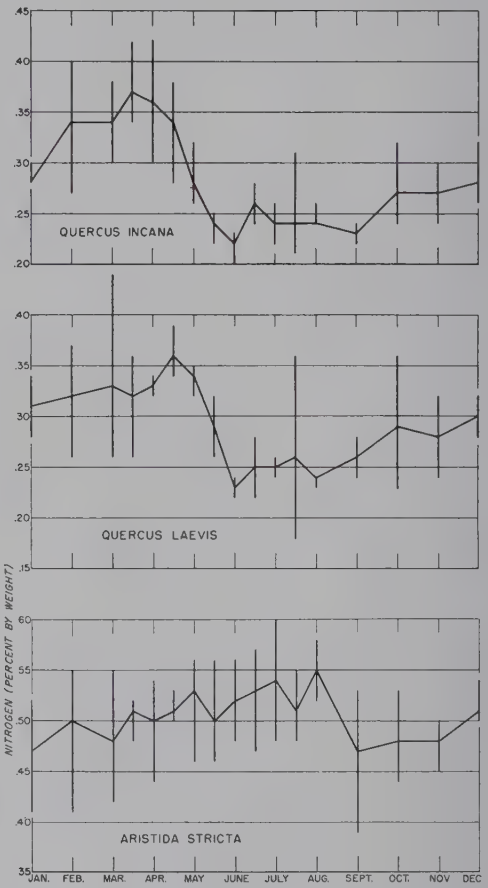
QUERCUS INCANA
QUERCUS LAEVIS
ARISTIDA STRICTA
NITROGEN (PERCENT BY WEIGHT)
JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV DEC

FIG. 2. Total nitrogen in roots of *Quercus laevis, Q. incana,* and *Aristida stricta.* Average of 3 years, 1954-1956. Vertical bars through curves indicate range of the 3 annual averages (1954, 1955, 1956).

around the first of February (Fig. 1). Differences between the average high and low points were not so great as for the two species of oaks. The time of least reserves in wiregrass came two months later than for the oaks.

Nitrogen reserves in wiregrass roots accumulated from September until August. Then they dropped sharply, perhaps because they were redistributed throughout the plant (Fig. 2). It was not possible to distinguish different vegetative phenological stages of the wiregrass. Because of the consistently brown color of the foliage, except for a short time following top removal, even the spring "green-up" is difficult to date.

Reaction to Tree Cutting

To determine the effect of tree cutting on root reserves, weekly root samples were taken in 1956 from undisturbed oaks, and from those whose tops had been cut off four inches above the ground. The tops were cut in early May, during the period of most active growth.

Beginning the second Monday of May, weekly samples of roots were taken for 13 weeks from predetermined pairs of trees at each of the two locations.

The reserve carbohydrates in roots of turkey oak and bluejack oak (Fig. 3) were decreased by cutting of tops. Differences between cut and uncut plants were apparent the first week after tops were cut. While the trees produced no sprouts during this week, their carbohydrate re-

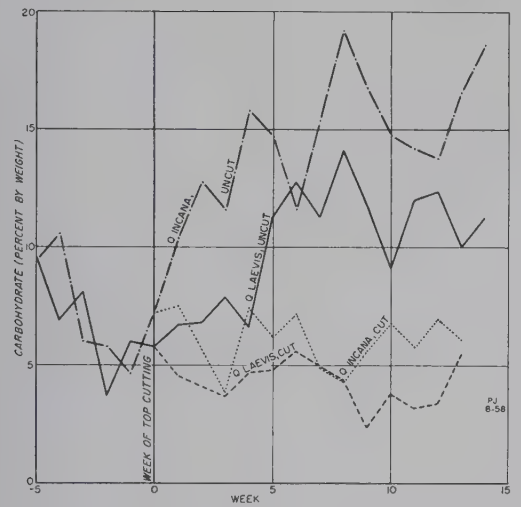

FIG. 3. Carbohydrate reserves in roots of cut and uncut oak plants, 1956.

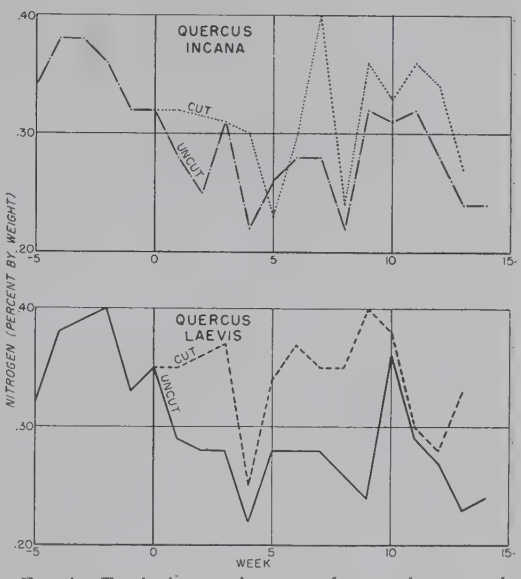

FIG. 4. Total nitrogen in roots of cut and uncut oak plants, 1956.

serves were probably lowered by normal respiration and root extension.

Differences between cut and uncut turkey oaks seemed to be greatest during the eighth week following cutting. Bluejack oaks showed large differences 3 weeks after cutting.

A "t" test of the differences in carbohydrates between cut and uncut plants revealed high statistical significance for both oak species.

Leaves of sprouts reached full size about June 18. They were deformed and extremely pubescent. Their phenological development varied so much that it could not be assigned to stages.

The per cent of nitrogen in roots of cut turkey and bluejack oaks (Fig. 4) remained fairly constant during the week following cutting. In the undisturbed oaks it dropped sharply, apparently because much of it was translocated to the new growth of leaves and stems.

The amount of nitrogen fluctuated considerably from week to week, but a "t" test revealed highly significant differences between the root reserves of the cut and uncut plants.

Summary and Conclusions

In a 3-year study in the sandhills of western Florida, carbohydrate food reserves in the roots of turkey oak and bluejack oak reached their lowest annual ebb between late April and early May. The period of greatest depletion coincided with the time the new leaves were reaching full size. The major nitrogen depletion period of oaks corresponded generally with that of carbohydrates, but lasted until about the first week of June.

Roots of pineland three-awn grass were at their lowest level of carbohydrates in mid-July and of nitrogen in September. Fluctuations of both carbohydrates and nitrogen were much less pronounced than in the oaks.

Cutting the tops from oaks caused the carbohydrates of the roots to remain low for at least twelve weeks.

From this study, it appears that late April or early May is the best time to start eradication of the oaks. Eradication treatment at the time probably would be satisfactory for the grass (which is of secondary importance), even though the root reserves of the grass are somewhat lower in midsummer.

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DIFFERENTIAL FOOD SELECTION BY MORAY EELS AND A POSSIBLE ROLE OF THE MUCOUS ENVELOPE OF PARROT FISHES IN REDUCTION OF PREDATION[1]

A mucous envelope which covers certain parrot fishes at night was described by Winn (1955). The mucus forms an ovoid envelope around the parrot fish at a distance from the body with an opening at the mouth and in back of the caudal fin. Such a conspicuous mucous fold might well protect the fish from predation at night.

Moray eels and sharks are the most notable night predators in the fish fauna of coral reefs. Morays especially move over the reefs from dusk to dawn, looking for carrion and live prey. Parrot fishes resting at night in protected areas or places on the bottom are extremely inactive and therefore might be an easy prey for such predators. We have undertaken experiments to test whether or not parrot fishes with a mucous fold are less liable to predation than parrot fishes without a mucous fold. Several species of parrot fish were used as prey. The first, *Scarus croicensis,* secreted a mucous fold and the others, several species of the genus *Sparisoma,* did not. The common spotted moray eel, *Gymnothorax moringa,* which inhabits the reefs where the parrot fish are found, was used as the predator.

The observations and experiments were initiated at the Lerner Marine Laboratory, Bimini, Bahamas, by the first author, and were completed at the Bermuda Biological Station, Bermuda.

Material and Methods

In each experiment (Tables I and II) one common spotted moray eel (*Gymnothorax moringa*) was placed in a tank with a small pile of rocks at each end. Three 36 × 18 × 18 inch stainless steel and glass aquaria were used at Bimini and two wooden tanks 48 × 20 × 15 inches, painted with black asphaltum on the inside and having a glass plate for observation on one long side, were used at Bermuda. The tanks were covered to prevent escape of the eels at night. Sea water flowed slowly through the tanks.

Six series of predator-prey experiments were carried out using 6 different moray eels and 5 tanks. The eels ranged approximately from 45 to 60 cm in total length. From one to 5 days after the morays were set in the tanks, 2, 3, or 4 individuals of *Scarus croicensis* and 2, 3, or 4 individuals of *Sparisoma radians* at Bermuda or *Sparisoma chrysopterum* at Bimini were added (Tables I and II). Also *Cyprinodon* sp. was used as prey with *Scarus croicensis* alone and together with a third species, *Sparisoma chrysopterum* (Table I). The prey individuals were always of nearly the same size. Every morning the prey fish were counted and those that had been eaten were replaced with new individuals of a comparable size. The moray eels ate these fish at night while they were all "sleeping" motionless on the bottom of the tanks. The aquaria were frequently checked just before dark and in the early morning. The results of each series of experiments are presented in Tables I and II and a summary of all experiments and all first day results is given in Table III. Chi-square significance tests were made with the table for minimum contrasts required in four-fold contingency tables by Mainland, Herrera and Sutcliffe (1956).

Table I. Predation by 3 individuals of the common spotted moray eel on 2 species of parrot fishes and a cyprinodont, Bimini, 1955. Fishes eaten at night were replaced so that the predator had a nocturnal choice of equal numbers of prey of all species

	Scarus croicensis Parrot Fish with Mucous Envelope	*Cyprinodon Sp.* Topminnow No Envelope	*Sparisoma chrysopterum* Parrot Fish, No envelope
Moray I			
March 8-13			
Total prey present..	18	18	
Total prey eaten...	1	7	
March 20-23			
Total prey present..	12	12	
Total prey eaten...	6	0	
March 25-26			
Total prey present..	5	6	5
Total prey eaten...	1	0	3
Moray II			
March 11-16			
Total prey present..	18	18	
Total prey eaten...	6	2	
March 22			
Total prey present..	3	3	3
Total prey eaten...	1	1	3
Moray III			
March 23			
Total prey present..	3		3
Total prey eaten...	0		2

Results and Discussion

There appears to be a marked tendency for the moray eel to prey on the species of *Sparisoma* more readily than on *Scarus croicensis.* The total difference in Table III is significant at the one % level. It seems likely that the mucous fold of *Scarus croicensis* reduces effective nocturnal predation by the moray eel. The moray uses primarily the senses of smell, taste and sometimes touch in its feeding activities. Smell is used for location of distant objects but when the front part of the head touches the food object an immediate and well oriented grasping due to taste and touch takes place and the food

[1] This is contribution No. 251 of the Bermuda Biological Station and was supported by a grant from the National Science Foundation to Dr. John E. Bardach. We wish to express our gratitude to the Director of the Bermuda Biological Station, Dr. William Sutcliffe, and to Mr. Brunell Spurling for assistance in making this study possible.

TABLE II. Predation by 3 separate common spotted moray eels on 2 species of parrot fishes at the Bermuda Biological Station, 1956. Fishes eaten at night were replaced so that the predator had a nocturnal choice of equal numbers of prey of all species

	Scarus croicensis Mucous Envelope	*Sparisoma radians* No Envelope
Moray I		
July 5-6		
Total prey present.	4	4
Total prey eaten..	1	2
July 14-15		
Total prey present.	8	8
Total prey eaten..	3	7
Moray II		
July 15-26		
Total prey present.	48	48
Total prey eaten..	7	19
Moray III		
July 16-26		
Total prey present.	39	39
Total prey eaten..	7	13

is swallowed. The grasping reflex is not initiated when the head of the moray touches the mucus and not the body of the fish. Twice mucus was placed in contact with the head of a blinded moray and no grasping or negative reaction occurred, but in several instances a blinded moray grasped a crushed or freshly dead fish when it was placed in contact with the predator's head. Apparently the mucus does not supply the proper taste and/or touch stimuli necessary to elicit the grasping response.

We could not discern any differences in the behavior of the two species of parrot fishes at night. They all remained nearly motionless on the bottom with greatly reduced respiratory movements and they could easily be picked up by hand. A behavioral difference may explain, however, why *Cyprinodon* was eaten as infrequently as *S. croicensis* (Table III). *Cyprinodon* were much more sensitive to disturbances than the parrot fish. This greater reactivity apparently made them as difficult to prey on as *S. croicensis* with the mucous fold.

TABLE III. Summary of the data presented in Tables I and II. The total prey offered and eaten in the first 24 hours cannot be seen in Tables I and II. Notations in brackets refer to levels of significance in Chi square tests

	Scarus croicensis Mucous Envelope	*Sparisoma spp. No Envelope*
Total prey offered.....	110	110
Total prey eaten.....	20	49 (1%)
Total prey offered on first day	23	23
Total prey eaten on first day.....	9	19 (1%)
	Scarus croicensis Mucous Envelope	*Cyprinodon No Envelope*
Total prey offered.....	56	57
Total prey eaten.....	15	10

Is it possible that the sparisomid parrot fishes are more palatable than *Scarus croicensis?* The morays did not entirely avoid the envelope secreting fishes at night and individuals of both types fed to morays during the day at Bimini seemed to be eaten readily. There were no observable differences in the way the morays grasped and ate both types.

The daily replacement of eaten fish with fresh individuals might have affected the outcome of the experiments since fish when first placed in a tank might be more readily eaten than those that have been in a tank for several days. If this were true one could expect more *Sparisoma* to be eaten. This is what happened but apparently for another reason. On the first day there was more predation on *Sparisoma* and the difference was significant at the one % level. This initial selection for *Sparisoma* persisted throughout the experiments and demonstrates that prey selection was not directed towards fresh or old tank residents but was due to a difference between the species.

At least 3 factors in the experiments might have operated against a selection for the species of *Sparisoma* and for selection of *Scarus croicensis,* the opposite of our results. Because of the eels' size and the limited space of the aquaria the moray could have brushed the mucous envelope away from the parrot fish. The lights were turned on in the laboratory on rare occasions at night and this caused the parrot fish to break out of their mucous folds. The moray could have eaten one before there was time to remake the fold in the dark. Toward the end of the experiments a careful check had to be made to see whether or not the ability to make the mucous envelope was lost because of starvation. A few parrot fish may have been in this condition. These factors probably would be eliminated in the natural environment so that the fold would be more effective in protection against predation. We cannot say at this time whether or not there is some slight ecological difference between the two types of parrot fishes that would lower the effective predation rate on the sparasomids which are not protected by mucous folds. Moray eels apparently eat parrot fishes as well as other species of fish which are more reactive to disturbances in the dark. In our experiments all 6 morays preyed more heavily on the parrot fish that did not secrete a mucous fold. Also, out of 26 counts at Bermuda more sparisomids were eaten during 17 nights, on 3 nights the number eaten of each species was the same, and during 4 nights more *Scarus croicensis* were eaten while no prey-fish were taken during the remaining 2 nights. It did not seem to matter which species of *Sparisoma* was offered although the data for the Bimini species were rather limited. These results and the fact that we did not find any difference between the species in behavior and palatability leads us to conclude tentatively that the mucous fold secreted around individuals of *Scarus croicensis* is effective in reduction of the predation rate by the common spotted moray eel. It is to be expected that this kind of protection might also work against other nocturnal predators.

SUMMARY

A series of predator-prey experiments were carried out with the common spotted moray eel as the predator. One

prey was either *Sparisoma chrysopterum* or *radians* offered together with *Scarus croicensis*. A mucous envelope is produced only by the last species and it was eaten less frequently. Tentatively we conclude that the mucous fold reduces effective predation by the common spotted moray eel.

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OYSTER SET OBTAINED IN THE NIANTIC RIVER, CONNECTICUT, ON CULTCH BUOYED NEAR THE SURFACE

The potential for a good set of oysters was discovered in 1955 in the Niantic River estuary in Connecticut. This was observed by suspending bags of oyster shell in the water and thus providing cultch or surfaces on which larvae might set if present. Chicken-wire bags containing the shell clutch were placed at 3 stations and were exposed for successive 4 day periods. At Station B, 0.6 nautical miles from the mouth of the estuary in a region of broad sand flats, the bags of cultch were suspended so that they remained within 1M of the surface. At Station D, 1.25 nautical miles from the mouth and with a depth of 3M, bags were rigged to remain within 1M of the bottom for comparison with others held within 1M of the surface. The same surface and bottom rigging was used at Station G, 1.95 nautical miles from the fall line and with a depth of 5M. The amount of setting by stations, depth, and date is given in Table I.

Table I. Oyster set—Niantic River 1955. First number is the count on the smooth surfaces of four shells. Number in parenthesis is a conversion to number per 100 square centimeters of cultch surface, calculated from approximate measurements of each shell examined

Date cultch was removed after 4* days' exposure on station	Station B Flats, lower River Cultch in 1st M only	Station D Mid-River Upper M	Station D Mid-River Bottom M	Station G Upper River Upper M	Station G Upper River Bottom M
June 6, 10, 14, 18, 22, 26, 30 July 4, 8..	None	None	None	None	None
July 12.....	**	5 (2)	None	118 (36)	None
July 16.....	3 (1)	31 (10)	1 (0)	48 (17)	None
July 20.....	1 (0)	5 (2)	None	22 (7)	None
July 24.....	None	None	None	3 (1)	None
July 28.....	None	2 (1)	None	None	None
July 31.....	None	2 (1)	None	1 (0)	None
Aug. 4.....	None	None	None	2 (1)	None
Aug. 8***.....	None	None	None	None	None
Aug. 13.....	None	2 (0)	None	None	None
Aug. 17, 21, 24 Sept. 1, 5, 9, 13....	None	None	None	None	None

*Occasionally the exposure period was varied slightly and this can be calculated by subtracting the preceding removal date from the one under consideration.
**Rig with cultch was missing on this date.
***Cultch kept at six Niantic River stations by the Milford Laboratory of the U. S. Fish and Wildlife Service for the period July 18 through August 9, 1955 showed set at only one station. This was a small count of 5 spat per 10 shells at a site near the middle of the River.

Hydrographic studies on the River, discussed more thoroughly in another report (Marshall in press), indicate a tendency toward stratification with surface circulation partially independent of deep waters for brief periods. This, coupled with the lack of set in deep water, suggests that the potential for oyster setting in the Niantic River may be confined to upper strata where, except for a few rocks and shells in a narrow belt along the shoreline, there is a dearth of natural attachment surfaces.

An inspection of the shoreline zone in the summer of 1955 showed oysters widely distributed. They appeared to be derived from several successive annual settings. They were not abundant and seemed somewhat stunted. If any good sets had occurred in former years, they had suffered heavy mortalities. Furthermore, the small size of the oysters suggested poor growing conditions. Specimens dissected and examined at the time by Charles A. Nomejko (then with the U. S. Fish and Wildlife Service Laboratory at Milford) were in good spawning condition.

Practical oystermen are constantly on the alert for sources of seed. One common proposal is to restore beds formerly very productive, as suggested by Loosanoff (1955) for certain estuaries of Long Island Sound. The observations on the Niantic River suggested that attention should also be given to areas that have never developed large beds simply due to the lack of suitable natural surfaces in the water strata where setting might take place. Relatively small and scattered populations of adults apparently have the potential for seeding such areas if cultch is suspended at the proper levels. Obviously, further observations are needed before depending on such a source and the set from such estuaries should be tried on various growing grounds to check against the possibility of an inferior, slow-growing stock.

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STUDIES OF TOLERANCE OF CERTAIN FRESHWATER FISHES TO BRINE WATER FROM OIL WELLS

Introduction

Several species of freshwater fishes are known to tolerate some degree of saltwater. Information regarding this tolerance is scanty, and usually concerns the spontaneous entry of fish into saltwater. The purpose of this report is to present data showing to what extent certain freshwater fishes can tolerate saltwater in a habitat from which they cannot escape. This study is based on field data and a limited amount of experimental data. Previously published data on the tolerance of certain species are brought together in this report.

History of the Problem and Description of the Area

For a period of about 2 years I have observed a pond, formed from the removal of earth to build a road. The pond is located about 20 miles north-east of New Orleans, Louisiana in St. Charles Parish, one mile north of U. S. Highway 61 on land known as Sarpy Wildlife Refuge. The pond itself is shaped in the form of a small letter "h." At the top of the "h" is a dense matting of weeds, the only possible avenue of escape from the pond. The weeds seem capable of prohibiting nearly all movement of fish into or out of the pond. During periods of extreme high water due to flooding caused by a hurricane, the weed area becomes flooded and probably permits the passage of fish. Under normal water levels the weeds probably allow some passage of small species or juveniles of larger-sized fish. The weed area remains intact throughout the year unless a hard freeze occurs to kill the weeds.

The pond has been under the influence of brine water from adjacent oil operations. Several oil wells are located in the vicinity and, adjacent to the pond, the crude oil from the wells is separated from the saltwater with which it comes to the surface as a mixture. The saltwater is pumped back underground, but occasionally backs up into an earthen impoundment built for this purpose. The impoundment seeps water which drains directly into the pond under study, thus raising the salt content of the pond. Data on fishes collected periodically from the pond are used in this report.

On one collecting trip, December 8, 1956, bowfin (*Amia calva*) and bullheads (*Ictalurus melas*) were observed swimming in shallow water, apparently under toxic influence, and were easily dipnetted. The salinity at the time of sampling was 16.5 $^{0}/_{00}$ and the water level very low. Some centrarchids were also observed to be in a weakened condition. During the following days the salt content continued to rise and more individuals of the above and other species died. On the night of December 12, 1956, a heavy rain filled thte pond and greatly reduced the salinity, but dead fish were still observed for the next 2 days.

Methods

Each day from the 8th through the 14th of December, 1956 all dead fish that could be found were collected and preserved in 20% formalin. Total measurements were recorded and averaged. Salinities were recorded for each collection. These data are listed in Table I. On December 16, 1956 the pond was rotenoned to determine what species remained. The pond was rotenoned a second time on March 15, 1957 to determine what fish if any had entered since December 16, 1956. Virtually no fish were collected on the latter date emphasizing the effectiveness of the weed bed as a barrier to the movement of fish.

During the period June to December 1957, several species in laboratory tanks were subjected to the saltwater from the wells. The object of the testing was to determine the lethal limits under experimental conditions, for some of the 20 species reported on in this study. The fishes used in the experiments were collected within a few miles of the study area and kept in 40 gallon tanks containing pond water from the collecting locality. After a few days (up to a week) a few fish were transferred into 10 gallon aquaria with the same pond water. The addition of brine water began about 3 to 5 days later. The delays were felt necessary to lessen the chance of death to fish from handling.

The salt content in the aquaria rose each day about 0.7 to 1.0 $^{0}/_{00}$ by the addition of brine water from the study area. The salt content was measured each day by hydrometer and corrected for temperature. The data were then converted to parts per thousand chloride ($^{0}/_{00}$) by means of the tables in Zerbe and Taylor (1953). No attempt was made to control the temperature of the aquarium water which varied from 24° to 28°C. All aquaria were examined at least once a day for dead or dying fish. The time of observation, hydrometer and temperature readings, record of brine water added and general condition of each aquarium were recorded each day. During the experiments the fish fed well on chopped earthworms and mosquitoe larvae.

Table I. Number and mean lengths of fish killed over a seven day period in December, 1956, in the study area. All lengths are in millimeters. The salinity for each day is given below the respective date.

	Dec. 8	Dec. 9	Dec. 10	Dec. 11	Dec. 12	Dec. 13	Dec. 14
Salinity	16.5	18.3	19.7	20.6	20.9	5.8	6.6
Species							
Amia calva	(29) 403.7	(1) 345	.....	.....	.....	.....	(1) 280
Ictalurus melas	(5) 163.4	(27) 139.5	(26) 138.9	(26) 124.3	(14) 127.0	(3) 114.6	.....
Notemigmus crysoleucas	.....	(1) 127	.....	.....	.....	.....	.....
Chaenobryttus coronarius	(17) 129.4	(52) 90.4	(156) 104.9	(119) 110.2	(136) 111.5	(127) 100.4	(134) 91.4
Lepomis symmetricus	(1) 43	(12) 58.8	(59) 57.8	(45) 59.2	(102) 58.1	(78) 59.2	(133) 56.0
Lepomis macrochirus	(2) 102.5	(2) 102.5	(51) 101.3	(104) 118.2	(63) 111.1	(133) 107.2	(168) 114.8
Lepomis cyanellus	(2) 151.0	.....	(3) 86.0	(1) 88	(6) 64.6	.....	(1) 97
Lepomis microlophus	.....	.....	(1) 105	.....	(2) 126.0	(1) 180	.....
Lepomis punctatus	(1) 141	.....	(4) 103.3	(1) 125	(8) 89.4	(4) 111.0	(8) 114.6
Micropterus salmoides	.....	.....	.....	(1) *	.....	.....	.....

*not measured

The salinities recorded prior to December 8, 1956 cover a 10-month period and varied from a low of 2.9 to a high of 10.1 $^0/_{00}$. Following the fish kill the salinity has varied from 13.7 to 22.0 $^0/_{00}$ during the spring. During the fall of 1957 as a result of flooding by a hurricane passing near the area, the salinity varied from 3.2 to 4.7 $^0/_{00}$.

Results

Twenty species representing nine families have been recorded from the pond. Each species will be discussed individually.

Since only the dead fish were collected each day, this procedure gives a reasonable estimate of the daily mortality. Live fish, frequently in poor physical condition, were noted each day through December 12, 1956. No fish of the several species killed by the high salt content were seen alive on December 13 and 14, 1956. Dead fish were recovered whether floating at the surface or lying on the bottom. Those on the bottom were generally fresh; those floating were bloated or in various stages of decomposition. During the last day no fish were found on the bottom of the pond. For this reason the last 2 day's collections could be considered together, as they probably comprise individuals that died a day or 2 previously.

1. *Amia calva.* Thirty-one specimens were collected and preserved. Two additional individuals were collected, one the first day and one the second day, but were neither preserved nor measured. Nearly all the specimens were collected alive, but in very poor physical condition. The fact that only two, both dead, were collected on the second day indicates that the salinity at the time was approximately the lethal limit. The specimen collected on the last day (December 14, 1956) was dead and badly decomposed. The bowfin appears to be able to tolerate some salt in its environment at least temporarily. It would be difficult, however, to approximate what the lethal limit of prolonged exposure might be. Although bowfin were not collected in the study area before or since the fish kill, the species is assumed to have been part of the permanent population. Bowfin are occasionally caught by hook and line in adjacent waters. A literature search has not revealed any other instance of bowfin surviving brackish water.

2. *Lepisosteus productus.* A single juvenile specimen of the spotted gar (218 mm in total length) was taken by rotenone on December 16, 1956. While spotted gars as well as other species of gars probably do occur in other pools or ponds in the swamp, this is the only specimen captured. The salinity at the time of this collection was 11.9 $^0/_{00}$. It is difficult to say whether or not this individual because of its small size entered the pond after the salinity reached the high of 20.9 $^0/_{00}$ or if it survived the high salinity.

3. *Dorosoma cepedianum.* Four gizzard shad measuring 305, 335, 340, and 355 mm in total length were taken when the pond was rotenoned on December 16, 1956. It is not surprising to find this species tolerating saltwater although it is more commonly found in fresh water. Gunter (1956) notes that the gizzard shad will enter sea water although it is considered a freshwater fish. It is commonly found in Lake Pontchartrain in brackish water. Kilby (1955) does not record this species from his studies on the Gulf coastal marsh areas of Florida. This species has not been collected in the study area at any time, nor from other areas of the refuge.

4. *Notemigonus crysoleucas.* One golden shiner was taken on December 9, 1956 when the salinity was 18.3 $^0/_{00}$. Although alive it was swimming erratically and appeared to be dying. This specimen is the only one ever taken in the area under study. Kilby (1955) reports it tolerating a salinity up to 5.6 $^0/_{00}$. The species apparently tends to avoid brackish water, however.

5. *Ictalurus melas.* In all, 101 black bullheads were collected. Although this species had not been collected prior to December 8, 1956, it is assumed to have been in the pond for some time. On the first day specimens were seen alive, but in poor physical condition. On December 9, 1956, the second day, only a few individuals were seen alive and these seemed to be in extremely poor condition. On the following day, the only observed specimens were dead and decomposing. On this basis a salinity of 18.3 is definitely lethal for this species. Probably a sustained exposure to a somewhat lower salinity would also be lethal as the bullheads collected the first day at a salinity of 16.5 were in poor physical condition. Clemens and Jones (1955) found the median toxicity threshold for the black bullhead to be 5.8 $^0/_{00}$. These data suggest that the lethal limit is probably lower than 16.5, possibly about 10 $^0/_{00}$. Lewis (in Clemens and Jones, 1955) records the black bullhead in the field at 2.2 $^0/_{00}$. Kilby (1955) records the closely related species *Ictalurus natalis* as occurring in waters at a salinity of 15.0.

6. *Anguilla rostrata.* Two individuals, 300 and 555 mm in total length, were collected from the pond, by rotenone on December 16, 1956. Since the eel lives part of its life in the sea, I assume it to have been present during the period of high salinity.

7. *Cyprinodon variegatus.* Specimens of the variegated cyprinodon have been collected many times both before and since the fish kill. During the high salinities none was seen dead; many were seen alive and in good condition. Simpson and Gunter (1956) found this species withstanding a salinity of approximately 142 $^0/_{00}$ in an evaporating tide pool. Individuals of this species certainly survived the period of high salinity.

8. *Fundulus pulvereus.* Although never taken in large numbers this species has been taken in nearly every collection. Simpson and Gunter (1956) recorded it in salinities of from 11.6 to 47.6 $^0/_{00}$. It is probably a permanent resident of the pond, and survived the period of high salinity.

9. *Fundulus chrysotus.* Two specimens of this species were collected on March 15, 1957 at a salinity of 13.7. Kilby (1955) collected two specimens at salinities of 15.0 and 24.7. Some experimental evidence has been accumulated on this species from 2 series of tests. In the first with 6 individuals, the fishes died at salinities ranging from 14.0 to 23.4. In the second test with 10 individuals, 6 died at salinities of from 13.6 to 30.6. Four individuals survived for 5 days after which the test was terminated. At this time the salinity had been raised from 1.7 to 30.6 $^0/_{00}$ over a period of 48 days. *F. chrysotus* can be said to tolerate rather high salinities for at least moderately long periods of time.

10. *Lucania parva.* Twenty specimens were taken on December 16, 1956 at a salinity of 11.9 $^0/_{00}$. This fish has been taken in marine environments at salinities of from 1.0 to 48.2 $^0/_{00}$ by Simpson and Gunter (1956) and 0.1 to 28.2 by Kilby (1955).

11. *Mollienesia latipinna.* The sailfin molly is by far the most abundant species in the study area and is present in all collections. Some specimens appeared in a weak condition the first day, but no dead or dying fish were ever collected. Further, live individuals were seen each day. One hundred and twenty-five specimens were taken

by rotenone on December 16, 1956. Again by rotenone, 850 individuals were taken on March 15, 1957.

Data are available from 2 tests. The fish began dying at a salinity of 20.3 $^0/_{00}$ in the first experiment and 20.1 in the second. Both tests were terminated with 2 individuals alive several weeks later at salinities of 38.1 and 35.0 respectively. The period of high salinity might have been lethal to a few individuals. Simpson and Gunter (1956) recorded *M. latipinna* in salinities of from 1 to 53.9. Kilby (1955) recorded this species over a range of 1.2 to 37.6 $^0/_{00}$. On the basis of the foregoing data, *M. latipinna* can be assumed with certainty to have survived the period of high salinity with little difficulty.

12. *Gambusia affinis.* Mosquito fish have been taken in nearly every collection in the study area. Thirty-four were taken on December 16, 1956 and 156 were taken March 15, 1957. These were at salinities of 11.9 and 13.7 $^0/_{00}$ respectively. Simpson and Gunter (1956) recorded the species at salinities varying from 1 to 20.6. Kilby (1955) recorded it from 1.2 to 25.2 $^0/_{00}$. No dead specimens were ever noted during the period of high salinity. *G. affinis* is certainly a permanent resident of the pond, and on the basis of the above data, is capable of surviving the adverse conditions.

13. *Heterandria formosa.* No specimens of this species were collected during the period of high salinity, nor in the rotenone collection of December 16, 1956. The species was collected at other times, the highest salinity being 13.7 for the rotenone collection on March 15, 1957. Kilby (1955) recorded *H. formosa* at salinities of from 0.0 to 15.0 but mostly below 4.9 $^0/_{00}$. Specimens tested in the laboratory died at salinities ranging from 5.2 to 14.1. The data indicate that this species will tolerate a moderate amount of salinity, but probably did not survive the period of high salinity. No dead specimens were noted, but since the species lives in weedy habitats, large numbers of individuals would have been difficult to find.

14. *Chaenobryttus coronarius.* Seven hundred and forty-eight specimens of this species were collected over the 7 day period. The mean total lengths for the period vary from 90.4 to 129.2 mm. On the basis of the size, there is no apparent selective killing of age groups by the high salt content. The largest number dead in any one day (156) were taken the third day and only dead individuals were observed after that. A salinity of about 19 to 20 is probably lethal to the species. Kilby (1955) never found *C. coronarius* at a salinity above 1.8 $^0/_{00}$, although it had ready access to the marshes. Apparently this form does not select a saline habitat and was present in the study area only because it could not escape.

Two tests were conducted on *C. coronarius.* In the first with 8 individuals death occurred between 10.7 and 15.7 $^0/_{00}$. In the second with 4 individuals death occurred between 13.9 and 16.9 $^0/_{00}$. This species can probably tolerate moderate salinities for some time. The estimated salinity of 19 to 20 is higher than the latter figures probably because of a greater rate of increase of salt content in the aquaria.

15. *Lepomis symmetricus.* This centrarchid is frequently represented in collections, possibly because it occurs in the shallower and more collectable areas. Only one specimen was collected the first day, but dead specimens were collected in increasing numbers throughout the period. Tests conducted on 2 groups of fish (4 and 10 individuals respectively) gave tolerances of 11.8 to 18.7 $^0/_{00}$ and 14.8 to 15.6 $^0/_{00}$ respectively. In the second test the brine water was added somewhat faster. Probably the length of time over which the salinity is raised to a certain level will vary the lethal threshold.

There does not seem to be any variable tolerance with respect to size of the individual. The mean lengths of specimens taken during the last 6 days are all within 3.2 mm of each other.

16. *Lepomis macrochirus.* As in the preceding species, there was a definite increase in the number taken over the period of high salinity. The mean daily lengths varied considerably, but it is difficult to make any interpretation of these data. Kilby (1955) found one group of this species in the marsh at a salinity of 5.6. I have taken this fish alive and apparently in good health at a salinity of 11.9 $^0/_{00}$.

Only one test was conducted on this species. Four juveniles, when subjected to an increasing salinity, died at salinities of from 13.9 to 16.9 $^0/_{00}$. The above collection of 11.9 was probably near the lethal limit.

17. *Lepomis cyanellus.* Thirteen specimens of this species were taken during the period of high salinity. One specimen was taken at a salinity of 8.9 eight months previous to the period of high salinity. Clemens and Jones (1955) found the median toxicity threshold of this species to be 3.8 $^0/_{00}$.

18. *Lepomis microlophus.* During the period of high salinity 4 dead specimens of this form were taken. It has never been collected prior to or since this period, although it probably occurs in other areas of the refuge. Kilby (1955) records *Lepomis microlophus* at salinities of 12.3 or less, mostly less than 5 $^0/_{00}$.

19. *Lepomis punctatus.* Twenty-six specimens of this species were taken during the fish kill. The species was not recorded before the fish kill, but was taken about a year later. Apparently it never reaches large numbers. It should be noted that the greater number of species were taken in the later days of the period of high salinity. Kilby (1955) has taken the species at salinities up to 11.8 but usually less than 5 $^0/_{00}$.

20. *Micropterus salmoides.* A single large specimen, not measured, was found floating dead on December 11, 1956. This species has not been taken by me before or since the fish kill, but local fisherman indicate that occasionally individuals are taken by hook and line. Kilby (1955) took one specimen at 11.5 $^0/_{00}$.

Discussion

Of the 20 species recorded from the study area all are thought to be permanent members of the population except for the catadromous eel which leaves to spawn. Ten species show a high tolerance to the brine water. These 10 species can be divided into 3 groups, partly based on Gunter (1956). The first group consists of fish directly of marine origin invading freshwater for part of its life (*Anguilla rostrata*). The second group is of marine origin but now living primarily in freshwater (*Dorosoma cepedianum*). The third group is derived from freshwater species. These species have or are presently invading the marine environment (*Cyprinodon variegatus, Fundulus pulvereus, F. chrysotus, Lucania parva, Mollienesia latipinna,* and *Gambusia affinis*). The remaining 2 species (*Lepisosteus productus* and *Heterandria formosa*) do not seem to be invading the marine habitat to any extent. Of the 10 species killed by the high salt content all are of freshwater origin and show little or no tendency to invade the marine habitat. Some of the centrarchids are occasionally taken in Lake Pontchartrain at low salinities, but they are not a major part of the lake population.

On the basis of the above considerations one might theorize that the fishes more closely related to marine species or the fishes that are at present expanding into

the marine environment are more tolerant of the periods of high salt content than fishes of freshwater origin.

Although there is no particular reason to expect any differences in tolerance to the brine water due to the size of the individuals, this aspect was investigated. For the 3 species taken in quantity (*Chaenobryttus coronarius, Lepomis symmetricus* and *L. macrochirus*) no selective kill was indicated with regard to total lengths. Keys (1931) has shown that freshwater representatives of *Fundulus parvipinnus* tend to have larger heads than the salt water forms. This aspect was not investigated.

Summary

Twenty species of fish were found to be living in a pond under the influence of brine water from oil wells. Two species (*Anguilla rostrata* and *Dorosoma cepedianum*) are of marine origin; the remainder are of freshwater origin. During a period of exceptionally high salinity 10 of these species were killed. Each species is discussed separately and the highest salinity at which the species was collected is given. Six species were experimentally subjected to brine water in laboratory tanks. Data on the laboratory determined lethal limits are compared to the field data. Conclusions are made about concentrations of brine water that certain species might survive.

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DISTRIBUTION OF EGGS BY *MICROBRACON* (HYMENOPTERA, BRACONIDAE)

The efficiency of a female entomophagous parasite in finding hosts and distributing her progeny is of considerable importance in the biological control of pest populations. It is now well established that the best results are obtained from using those parasitic species that are capable of finding hosts at low densities. However, this host-finding ability must also be coupled with an economical distribution of progeny, and it is known that many such parasitoids are able to discriminate between hosts that are suitable for the development of progeny and those that are not. This discriminatory ability with its attendant restraint in oviposition prevents a wastage of progeny, for the females tend to avoid ovipositing in hosts that are already parasitized. This restraint is not absolute, however, and breaks down under certain circumstances.

An analysis of the efficiency of *Microbracon hebetor* Say in the distribution of its progeny was made by Ullyett (1945). He discovered that the female parasite was remarkably efficient in being able to distribute her eggs in accordance with the relationship between the size of the host and the number of her progeny that can develop thereon. He found, however, that this does not hold under conditions of low host density because, according to him, the parasite is not able to exercise restraint in egg laying. Ullyett concluded that efficiency in distribution increases in direct proportion to host density.

Recently an opportunity arose to apply the experimental techniques of Ullyett on another species of *Microbracon*. This species has not been positively identified, but appears to be a segregate intermediate between typical *M. brevicornis* Wesm. of Europe and typical *hebetor* Say of the Western Hemisphere. It does not produce progeny in matings with *hebetor*. The stock was obtained from India where it had been reared on *Corcyra* and it is a typical external parasite of lepidopterous larvae. The deposited eggs are easily seen and counted under relatively low magnification of a stereoscopic microscope.

The condition's of Ullyett's experiments were duplicated in that there were five series (**A** to **E**) in which 2, 4, 6, 8, and 10 hosts were supplied respectively to each female parasite during a 24-hour period. The hosts were full grown larvae of *Ephestia kühniella* Zeller. Parasites and hosts were confined in Syracuse watch glasses of a standard size. They were kept at a constant temperature of 80°F. Although Ullyett indicates neither the condition nor age of his experimental animals, the parasites used in the present study were all freshly emerged females at the time each replicate was started. There were 5 replicates of each series. Daily records were taken for each female parasite for a 10-day period.

Differences in behavior between Ullyett's *hebetor* and the Indian segregate were immediately evident. Ullyett found that the search of the environment occurred in two distinct phases, namely (a) the search for all the living hosts and their paralysis when found; (b) a second and distinct search to relocate these immobile larvae in order to use them for egg laying. The Indian form does not exhibit this behavior, but instead normally finds, paralyzes, and oviposits on a single host before abandoning it. The female may, however, later return to the same host individual and repeat oviposition if she has not been successful in locating other unparasitized hosts.

The records of oviposition of the Indian *Microbracon* were drawn up (Table I) in the form of a frequency distribution exactly as was done by Ullyett for *M. hebetor*, and, for comparative purposes, his figures are given in parentheses. Although the mean numbers of eggs per host were higher in the present experiment the trend in distribution of eggs as host numbers increased was similar to the pattern described for *hebetor*. Ullyett found that a progressive change in the shifting of the

TABLE I. Microbracon: Distribution of eggs (Figures in parentheses are data from Ullyett, 1945)

No. of Eggs Per host	No. of Host Larvae: Series A 2 Hosts	B 4 Hosts	C 6 Hosts	D 8 Hosts	E 10 Hosts
1	2	2 (3)	7 (4)	11 (13)	21 (28)
2 - 3	4	12 (7)	30 (26)	34 (63)	57 (69)
4 - 5	4 (3)	18 (12)	30 (49)	40 (50)	59 (62)
6 - 7	9 (3)	12 (25)	34 (33)	39 (32)	40 (20)
8 - 9	10 (19)	29 (25)	26 (21)	26 (5)	27 (6)
10 - 11	14 (6)	31 (17)	26 (3)	17 (1)	14
12 - 13	11 (6)	16 (5)	6 (2)	11 (1)	5
14 - 15	13 (4)	18 (1)	11	10	—
16 - 17	12 (3)	7	9	11	5
18 - 19	6 (3)	5	1	3	2
20 - 21	2 (1)	4	—	—	1
22 - 23	3	1	1	—	1
24 - 25	1	—	—	1	—
26 - 27	1	—	—	—	—
28 - 29	—	—	—	—	1
Means per Host	12.20 (9.25)	9.94 (5.79)	7.55 (5.14)	7.25 (3.96)	5.75 (3.49)
S. D.	5.51 (3.87)	4.64 (2.56)	4.33 (2.35)	4.57 (2.23)	4.09 (0.76)
S. E.	0.55 (.55)	0.37 (.263)	0.32 (.20)	0.32 (.17)	0.27 (.056)

mode took place up to approximately the series **D** in which 8 hosts are available, and then the mode remains constant even though more hosts are supplied.

Ullyett believed that the female deposited the optimum number of eggs on each larva and then, by re-encounters with the same larva in her wanderings in the environment, repeated the oviposition. He assumed that the maturation of eggs in the ovaries produces a physiological urge which cannot be denied although the parasite may recognize the presence of eggs on a host which is visited. Accordingly, from his experiments he concluded that there was no exercise of any restraint in oviposition. In the present experiment, however, data obtained on the number of eggs deposited per female per day (Table II) show that some degree of restraint is exercised until a total of 4 hosts are supplied, then the egg laying rate becomes fairly uniform.

The data in Table II also show that the production of eggs by a female does not reach its normal level until the third day after emergence. This was true of all the

TABLE II. Restraint in oviposition at low host density, and effect of age on egg production

Mean No. eggs/♀/24 hours

Series: No. Hosts Supplied	Day of Oviposition 1	2	3	4	5	6	7	8	9	10	Mean
F: 1 host	12.0	11.25	20.5	27.2	20.3	19.0	21.3	21.7	17.0	22.0	19.2
A: 2 hosts	11.2	12.0	27.6	25.4	25.2	23.6	29.4	22.0	24.2	27.4	22.8
B: 4 hosts	12.6	16.4	34.8	33.4	33.6	33.4	40.8	29.0	34.2	39.8	30.8
C: 6 hosts	6.6	14.4	35.0	24.2	31.4	25.8	40.0	27.4	27.0	39.0	27.0
D: 8 hosts	6.4	15.8	29.0	27.6	33.0	34.6	43.0	31.0	31.8	43.6	29.6
E: 10 hosts	8.6	13.0	29.2	29.4	31.8	31.4	36.2	27.2	33.8	45.3	28.6
Mean	9.57	13.81	29.35	27.87	29.21	27.97	35.1	26.38	28.0	36.18	

females in each series, and thus is independent of the number of hosts (ovipositional sites) available. This fact is worth noting for the use of females of unequal age would introduce an undesirable variable into any critical experiment on progeny distribution.

SUMMARY

The experimental set-up used by Ullyett (1945) in his study of progeny distribution by *Microbracon hebetor* Say was duplicated in order to compare the distribution of eggs by a *Microbracon* species from India. The general pattern of egg distribution was found to be similar, but differences in behavior of the 2 species were noted, for the Indian species, unlike *M. hebetor,* paralyzes a host and oviposits on it before proceeding to seek another host individual in the environment. Furthermore, the mean number of eggs deposited per host by the Indian segregate is greater than in *M. hebetor,* and the Indian species does exercise some restraint in ovipositing on previously parasitized individuals. The importance of the age of the female parasite in any critical and quantitative study of egg distribution is emphasized.

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MORTALITY OF LOGGERHEAD TURTLE EGGS FROM EXCESSIVE RAINFALL[1]

During the early summer numerous Atlantic Loggerhead turtles (*Caretta caretta caretta* Linné) nest on the beaches of the Georgia sea islands. The following observations were made on a beach about 3 miles long on the southern part of Sapelo Island, Georgia. Trails of the turtles on the beach, the nests themselves, and rarely the female turtles in the act of depositing eggs were observed on this beach during the years 1954-1957 (Table I). The limits of the nesting season were 19 May to 15 July. Trails were most frequent during the last week of May and the first 3 weeks of June. Although drifting sand occasionally could have obliterated some of the trails before they were found, it is believed that the majority of them were observed.

All of the nests that were located were caged with ¼" mesh screen. The screen was set into the sand to a depth of about one-half meter, and a space of 5 to 10 centimeters was left between the surface of the sand and the top of the cage so that the young turtles could emerge from the sand. The caged nests were then kept under observation in order to determine the incubation period of the eggs. Of 17 nests caged, only one, in 1954, produced young turtles. Emergence from the sand occurred over a period of 5 days from 63 to 68 days after

[1] Contribution number 9 from the Marine Institute of the University of Georgia, Sapelo Island, Georgia. This research was supported by funds from the Georgia Agricultural and Forestry Research Foundation.

TABLE I. Loggerhead trails observed on beach of Sapelo Island

Year	Number trails observed	Nests found	Nests possibly present but not found	Turtle did not lay
1954	2	2		
1955	7	2	3	2
1956	4		4	
1957	19	13	3	3

deposition. Some eggs from the other 1954 nest were transplanted to a sandy location behind the University of Georgia Marine Institute, about one-half mile from the beach, where hatching occurred in 61 days. Caldwell, Carr and Hellier (1956) report incubation periods of 57 and 68 days for transplanted loggerhead eggs. Carr (1952) gives 31 to 65 days as the incubation period for eggs of *C. c. caretta*.

MORTALITY

Fifteen out of the 17 caged nests failed to produce young turtles. These failures represented all the nests under observation in 1955 and 1957. No nests were found in 1956. The cause of this catastrophic mortality was drowning of the eggs by fresh water from excessive rainfall.

In 1955, eggs were laid on 10 and 15 July; these nests are designated as 55-1 and 55-2. On the basis of an incubation period of 60 days or more these eggs should have hatched on 8 and 13 September or later. Prior to 11 September rainfall was about normal for this area (see Table II for mean rainfall pattern), but on 12 and 13 Sapelo Island received 6.48″ and 8.30″ of rain respectively. The soil was completely saturated, and there was standing water in all low areas on the island for 2 or 3 weeks thereafter. On 19 September the nests were excavated. Anaerobic conditions prevailed in nest 55-1; the eggs were blackened, and there was a strong odor of H_2S. Of 3 eggs opened, 2 contained dead embryos which apparently had been nearly ready to hatch. The eggs in nest 55-2 were still flooded by fresh water and were partly decomposed.

To establish the source of the water which had flooded the nest, a series of holes was dug in a line normal to the beach and a water sample collected from each hole. The water level profile and salinity distribution are shown in Figure 1. A similar profile was determined on 2 October 1957 (Fig. 1). During the 5 days preceding this date 5.92″ rain fell and high tides flooded the back beach. Despite the flooding by sea water the water in the sand in the back beach was quite fresh and there

TABLE II. Rainfall averages (inches) for Sapelo Island and vicinity, years of record in parentheses

Month	Sapelo Island (4)	St. Simons Island, 25 miles south Sapelo (17)	Blackbeard Island, 6 miles north Sapelo (10)
July	4.76	6.34	5.05
August	4.16	5.80	6.15
September	11.61	10.55	8.00
October	4.37	5.13	2.66

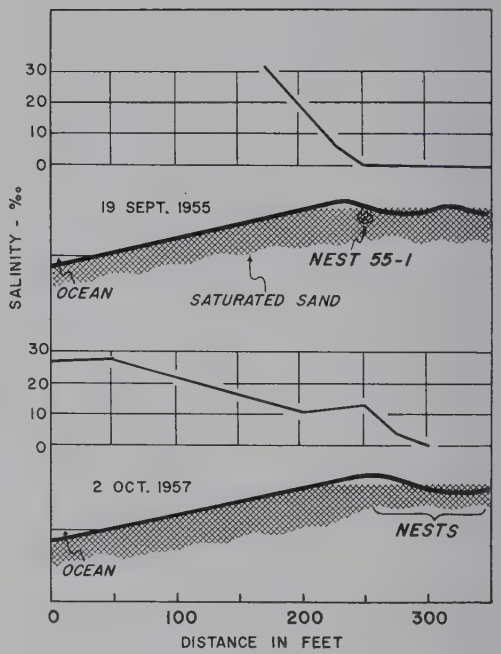

FIG. 1. Cross sections of beach showing level of ground water (cross-hatched) and distribution of salinity in ground water.

was visible surface seepage on the lower portion of the fore beach. These two profiles demonstrate the complete saturation of the beach sand by subsurface drainage following heavy rains.

In 1957, 13 nests were caged, the earliest on 19 May and the latest on 11 July. The eggs in the first nest, 57-1, should have hatched shortly after 18 July. During the period 25-29 July rainfall totalled 4.87″. On 1 August nest 57-1 was excavated and found to be flooded with water about halfway up the nest cavity. The eggs had started to decompose, anaerobic conditions existed, and the surrounding sand was black. On 8 August, nest 57-2 was excavated and the same situation found except that the water level had receded to slightly below the eggs. The water had a salinity of less than 0.02 $^{0}/_{00}$. The flooding occurred 56 days after the eggs were deposited. These eggs were all examined; 44 contained no embryos and were apparently infertile; 43 contained late embryos, all of which were dead. From their stage of development it is quite probable that they died about the time of the heavy rainfall.

Nest 57-3 was excavated on 6 August, 67 days after deposition, and the eggs were found to be in an early stage of decomposition. Ninety out of the 116 eggs in the nest contained late embryos, all dead.

Nest 57-6 was excavated on 20 July, 36 days after deposition and 5 days before the heavy rain. Two eggs removed for examination contained about half developed, living embryos. Although this particular nest was later lost by being covered with wind blown sand and so could not be re-excavated, the area was kept under surveillance long enough to be reasonably certain that no turtles emerged.

One other nest is of interest in establishing the schedule of the mortality. Nest 57-12 was dug up on 29 August, 49 days after deposition. All 125 eggs were fertile and contained very early, dead embryos. These eggs were only 14 days old at the time of the heavy rain. Several other nests from intermediate dates were examined; none of them contained living embryos.

From the stage of development of the embryos from this series of nests it appears fairly certain that the mortality occurred in late July at about the time of the heavy rainfall. Furthermore since all the nests but one were located in the flat area on the back beach, the presence of water in 2 of the nests was a fairly good indication that all the nests were probably flooded with fresh water. The exception was a nest located in the side of an old dune in a narrow portion of the beach. Unfortunately this nest was destroyed by a northeast storm. Thus there were no successful nests on this particular beach in 1957.

Rainfall Pattern

All available rainfall records for Sapelo Island and two other nearby islands are given in Table II. At Sapelo Island heavy rains have occurred during the first 2 weeks in September in 3 out of the 4 years of record. Considering the longer records from Blackbeard Island and St. Simons Island, this wet period seems to be a characteristic of the climate of this coast. These heavy September rains were not due primarily to hurricanes which rarely strike this particular coast.

Conclusion

During most years eggs laid by the third week in June would probably produce young. Eggs laid after 1 July would have a poor chance of survival in most years because of the September rains. Since the eggs in both 1955 nests were deposited after 1 July, the mortality was to be expected. However, the 100% mortality of Loggerhead eggs observed in 1957 was unusual in that it resulted from excessive July rainfall concentrated in a period of a few days.

Acknowledgement

The author is indebted to Dr. Bernard S. Martof of the Department of Zoology, University of Georgia and Dr. David K. Caldwell of the U. S. Fish and Wildlife Service for reading the manuscript and offering helpful suggestions.

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OXYGEN ANOMALIES IN THE SURF NEAR COOS BAY, OREGON[1]

It is generally assumed that inter-tidal and other shallow water sessile organisms located in and near the surf are bathed in ocean waters that are at or near saturation with dissolved oxygen. Oceanographic observations from outside the surf zone usually show that the surface waters are saturated with oxygen except during times of intense upwelling of undersaturated waters from below. Sea water entering shallow coastal estuaries under the influence of density currents and tidal mixing is also assumed to be saturated with oxygen, such that any oxygen sag is assessed to respiration within the estuary.

The results of occasional random sampling on the Oregon Coast and a Study by E. A. Pearson (Unpublished) in the mouth of Grays Harbor, Washington, suggest that the above conditions may not always exist. For this reason, a study was made of a large group of unpublished oxygen data taken in and near the Coos Estuary on the Oregon Coast.

The data which form the basis for this study were taken by John Queen at approximately bi-weekly intervals on 47 different days over a 27-month period in 1930, 1931, and 1932. Three to 5 water samples were taken at each station at approximately 3-hour intervals. All samples were taken at time of high or low water or halfway between.

Surf samples were taken at 2 stations located on small pocket beaches 1¼ and ¾ nautical miles south of the entrance to the Coos Estuary. Data from these 2 stations were grouped together (except for 9 days when data were available for one station only). The mean oxygen concentrations are plotted on the top broken line on Figure 1. Each point is based on from 4 to 10 individual observations with a mean of 7.8 observations per day. The minimum concentration observed at either station during any one day is also plotted for those days when very low oxygen concentrations were observed.

Water temperature and salinity data were collected for each water sample for an oxygen determination. The mean water temperature and mean salinity for the 2 surf stations are plotted as broken lines in the center of Figure 1.

Annual Cycle

Consistently low oxygen concentrations were found in the surf from January to the middle of May each year. Relatively high concentrations were recorded during the rest of the year. Only a few of the mean concentrations are near the saturation range of 5.5 to 6.5 ml/1. The highest concentrations occurred during August and September. The mean per cent saturation for the whole 27 months was approximately 65%.

The individual minimum observations each day approach 2 ml/1 during January, February, and March down in the range where damage may occur to some organisms.

[1] This work was supported in part by an Office of Naval Research Contract and by Oregon State College.

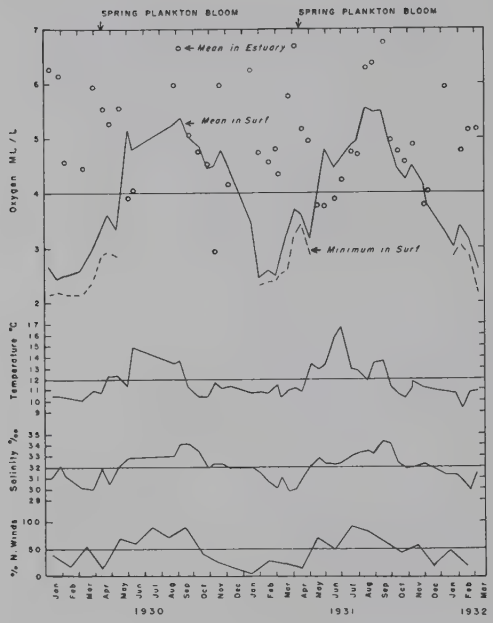

FIG. 1. Oxygen, temperature, salinity, and wind data for the Coos Bay area.

ESTUARY AS A SOURCE

One possible source of water low in oxygen is the estuary. The oxygen data from two stations located 8 and 11 nautical miles up the channel in the estuary were averaged together for each day and plotted as circles on the top of Figure 1. Both surface and bottom data were used to give an average of 16.8 individual observations each day or a total of almost 900 for the whole period. Note the lack of correlation between the surf and estuary data. It is apparent that the estuary is not the major source of de-oxygenated water during late winter and spring.

It has also been suggested that the anomously low oxygen concentrations may be due to the oxygen demand of decaying organic matter, but it is hard to estimate the source of the large amounts of material needed to bring about the observed conditions during the winter months.

UPWELLING

A better estimate is that these low oxygen concentrations must be related to upwelling of sub-surface ocean water. The problem here is that it occurs at the wrong time of the year. According to Sverdrup, *et al.* (1946) and Reid, *et al.* (1958), upwelling should occur off Oregon when the wind has a component from the north for protracted periods of time. Reid, *et al.* (1958), states that the atmospheric pressure systems should be in such a position that upwelling is most likely to occur off the Oregon Coast during August. But this is the month where maximum oxygen concentration occurs in our data. The long-term mean pressure charts show prevailing southwest winds off Coos Bay during February, the time when minimum oxygen concentrations were observed during 1930 and 1931.

A check was made to see if 1930, 1931, and 1932 were unusual years from the standpoint of wind direction. Daily historical surface weather maps (U.S. Weather Bureau) were examined for the 27-month period when oxygen observations were made. The days with a northerly component to the geostrophic wind were tabulated by months for 42.5° N. Lat. between 125° and 130° Long. The per cent of days out of each month with winds with a northerly component is plotted as a broken line at the bottom of figure 1. These data show that the winds follow the long-term average pattern as far as the northerly component is concerned. North winds do not prevail during the months with low oxygen. This should occur if the primary cause of the low oxygen concentrations were the accepted type of upwelling.

An examination of oceanographic data from offshore shows that if the low oxygen water (< 3 ml/l) were recently upwelled, it would have come from a depth range of from 75 to 200 meters. If this were the source, the salinity should be greater than 33.9 $^{0}/_{00}$, and the temperature less than 7.9°C. This range of salinity is only approached during late summer (Figure 1) while the mean water temperature was above 10°C in the surf during the time when low oxygen concentrations were observed.

Reid, *et al.* (1958), pointed out that spotty upwelling occurs at all times of the year at several locations along the California Coast. They attribute this in part to a combination of ocean currents and local topography. This appears to be the most logical explanation for the low concentrations which are found in winter off Coos Bay, although the exact mechanism is not understood. The upwelled water would have to be mixed with fresher and warmer surface water in order to have the observed distribution of salinity and temperature.

SUMMARY AND CONCLUSIONS

Anomalously low oxygen concentrations are reported for the surf near the entrance to Coos Bay, Oregon. Low oxygen concentrations were found from January through May and relatively high values the rest of the year. The times when low concentrations were found does not correlate with the expected time of maximum upwelling. The low concentrations do not appear to be caused by de-oxygenated water coming out of the estuary.

It is suggested that the possibility of low oxygen concentrations in the surf must be considered as an ecological factor in the study of shore life.

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A DISCUSSION OF THE IMPORTANCE OF THE SCREEN SIZE IN WASHING QUANTITATIVE MARINE BOTTOM SAMPLES[1]

Since Petersen and Jensen (1911) initiated quantitative marine benthic studies, there has been a continual and increasing interest is such programs of research. This is the result of a general increase of interest in the ocean (Hiatt 1954), the desire to compare the benthos of different seas (Thorson 1955), a method of obtaining animals to learn what organisms are present within an area (Hartman 1955), or because of the importance of the benthos to the study of marine pollution (Reish 1955).

Frequently, techniques and sampling equipment vary; thus we have, for example, the Petersen grab (Petersen and Jensen 1911), Van Veen (Thamdrup 1938), Holme scoop-sampler (Holme 1949), Eckman grab (Miyadi 1940), and various sizes of the Hayward orange-peel bucket (Lee 1944, Reish 1955, Hartman 1955). The efficiency of different samplers have been compared, for example, by Thamdrup (1938) and there have been attempts to standardize the type of bottom sampler used (Thorson 1955). Equally varying has been the size of the mesh opening used for washing the collected sample. Since the bulk of the sample consists of sediments, it is necessary to wash this material in order that the organisms can be seen and studied. A mesh opening of 1.5 mm has been the most frequently employed screen (*e.g.* Petersen and Jensen 1911, Idelson 1930, Mistakides 1951, Davis 1923. However, screens with an opening as large as 2.2 mm (Holme 1953) or as small as 0.2 mm (Moore 1931) have been used in various types of studies. The importance of the mesh opening in washing the sample has not been emphasized in the past. Saunders (1956) considered the opening of the screen in comparing his results with those of others. The purpose of this report is to emphasize the importance of the size of the screen in washing quantitative samples. It is as important to consider what is done with the sample once it has been collected as to consider the method of taking the sample.

Materials and Methods

Five samples were taken in a line from floating docks in Alamitos Bay, California. The depth of the water was about 15 feet mean low water. The samples were collected with a size one Hayward orange-peel bucket (Reish and Winter 1954) which takes a grab covering on area of 650 cm^2. The volume of the sample ranged from 2 to 3 liters. The samples were spaced at about one to 2 foot intervals in order to minimize the possible differences due to patchiness in distribution or variations in substrate type. The substrate was a fine gray mud in all 5 samples. An area possessing this type of substrate was chosen in preference to a sandy bottom since all the fine mud particles would pass through the finest screen used. The sample was emptied into a tub and then transferred to one-gallon jars. The material was preserved with full strength formalin and transported to the laboratory.

The samples were washed separately through a series of 11 graded Tyler screens. These screens fit into one another and measure 20.5 cm in diameter. The sizes of the screens used, as measured by the number of openings per inch, were 4, 7, 12, 16, 20, 24, 28, 32, 42, 60, and 100. The dimensions of the screen openings were 4.7, 2.8, 1.4, 1.0, 0.85, 0.7, 0.59, 0.5, 0.35, 0.27, and 0.15 mm.

The specimens retained on each screen were handled separately. The biomass was determined by wet weighing the material retained on each screen. Worm tubes and molluscan shells were considered as part of the biomass. The numbers of species and specimens were determined separately for the material retained on each screen.

[1] This research was supported by research grant (E-556 [C4]) from the National Institutes of Health, U.S. Public Health Service to the University of Southern California.

Results

The data are summarized in Table I and Figure 1. Table I lists the species of animals collected and the total number of specimens for the 5 samples retained on the individual screens. Figure 1 summarizes the data graphically giving the biomass, the number of species, and the number of specimens for the 5 samples. The data in Figure 1 are cumulative to indicate where the plateau is reached for each factor considered.

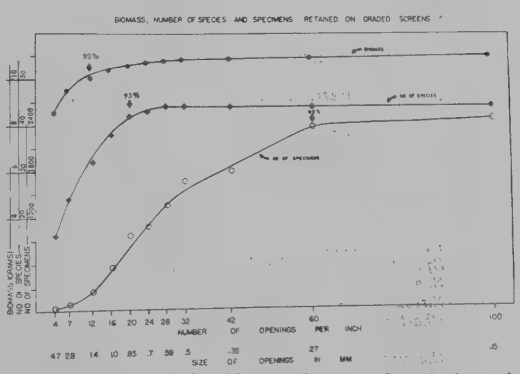
BIOMASS, NUMBER OF SPECIES AND SPECIMENS RETAINED ON GRADED SCREENS
92%
93%
BIOMASS (GRAMS)
NO. OF SPECIES
NO. OF SPECIMENS
4 7 12 16 20 24 28 32 42 60 100
NUMBER OF OPENINGS PER INCH
47 28 14 10 85 7 59 5 35 27 15
SIZE OF OPENINGS IN MM

FIG. 1. The relationship of biomass, the number of species, and the number of specimens to the size of the screen opening used in washing quantitative marine bottom samples.

Biomass.—This is defined as the weight of the animals retained on the screens. In this case, the results indicate the wet weight in grams including worm tubes and shells of living molluscans. The biomass is given in Figure 1 and represents the average for the 5 samples. It is seen that most of the biomass is retained on the larger screens. Over 90% of the biomass is retained by screen 12. This is composed largely of a few individuals such as the pelecypods (*Macoma nasuta*) and the larger polychaetes (*Diopatra splendidissima, Amaea occidentalis,* and *Pista alata*).

Number of Species.—Forty-two species of animals were encountered. The data given in Figure 1 are the totals for the 5 samples. All but 2 species, or 93%, were encountered by screen size 20. Nematodes were first collected from screen size 24, and a single decapod larva was retained on screen 28.

Number of Specimens.—A total of 2479 specimens was collected in the 5 samples. Two forms accounted for 58% of this total, 866 *Cossura candida* and 581 nematodes. Both of these were small in size. The nematodes were first collected from screen 24 and reached maximum numbers on screen 60. *Cossura candida* was first observed on screen 12 and reached maximum numbers on screen 32. The plateau in the curve for number of specimens was not reached until screen 60; this was influenced considerably by these two forms.

First Appearance of Species.—Of considerable impor-

TABLE I. Number of specimens retained on graded screens

No. openings per inch Size of opening in mm	4 4.7	7 2.8	12 1.4	16 1.0	20 .85	24 .7	28 .59	32 .5	42 .35	60 .27	100 .15	
Species												Total
Phylum Nematoda												
nematodes, unidentified						1	2	6	26	476	90	581
Phylum Nemertea												
nemerteans, unidentified	2	7	6	3	5	2		1				26
Phylum Annelida												
Class Polychaeta												
Eteone dilatae Hartman		1		1	1							3
Eumida sanguinea (Oersted)				1								1
Podarke pugettensis Johnson					1			1				2
Exogone sp.					1							1
Neanthes caudata (delle Chiaje)		1										1
Platynereis bicanaliculata (Baird)				1		1						2
Nephtys caecoides Hartman			2									2
Diopatra splendidissima Kinberg	1											1
Lumbrineris erecta (Moore)	4		2									6
L. minima Hartman	4	10	31	9	3							57
Dorvillea articulata (Hartman)			22	52	30	5	4	2	2	2		119
Haploscoloplos elongatus (Johnson)	1	1	8	6	2			1	1	1		21
Laonice cirrata (Sars)	1	1										2
Nerinides acuta (Treadwell)			2	9	1							12
Prionospio cirrifera Wiren	1	6	23	100	115	30	18	10		1		304
P. sp.				1	3	1						5
Spiophanes missioniensis Hartman	1	1			1							3
S. sp.		2	1	3	1							7
Streblospio benedicti Webster			3	2	3			1				9
Chaetozone corona Berkeley		1	1	1								3
Cossura candida Hartman			1	11	129	100	157	265	88	105	10	866
Tharyx parvus Berkeley	1	5	3	1		2						12
Pherusa capulata (Moore)			2	3	5	1	1					12
Asychis disparidentata (Moore)		1										1
Armandia bioculata Hartman			2	2	3	2	1	1	1	1		13
Capitella capitata (Fabricius)		1										1
Capitita ambiseta Hartman	3	6	29	104	109	23	21	13	2			310
Amaea occidentalis Hartman	2	8										10
Pista alata Moore	3				1							4
Euchone sp.			3	7	8	3	9	3	2	3	2	40
Phylum Arthropoda												
Subphyllum Crustacea												
copepods, unidentified					2			3	5	3		13
Crangon californiensis (Holmes)	3											3
decapod larva, unidentified							1					1
Phylum Mollusca												
Class Pelecypoda												
Chione undatella (Sowerby)				1								1
Macoma nasuta (Conrad)	4	4	3	2				1				14
Tagelus californianus Conrad	1			1								2
clam, unidentified			4									4
Class Gastropoda												
Acteocina smira Dall				1								1
tectibranchs, unidentified					2							2
Phylum Chordata												
Class Pisces												
fish, juvenile, unidentified	1											1
Totals	33	56	148	322	426	171	214	308	127	572	102	2479

tance in quantitative studies are the screen sizes at which animals first appear and later disappear. These data are included in Table I. A hyperbolic curve would be obtained if the data for the first appearance of the species were plotted. As stated above, only 2 species appeared for the first time on screens smaller than size 20. A somewhat flattened normal distribution curve would be obtained if the data for the last appearance of species were plotted. The peak of disappearance was reached at screen 20, but 3 species were taken on screen 100.

Discussion

The results of this study indicate the importance of considering the size of the smallest screen employed in washing samples collected from a quantitative survey. The amount of time involved in working the sample increases with the fineness of the screen opening. Therefore, the size of the smallest screen may vary according to the purpose of the survey. If the purpose is only to record the weight of the organisms occurring on the bottom, then only a large screen needs to be used since the majority of the biomass is due to a few large animals. A slightly smaller screen should be employed if the purpose is to record a list of the species occurring in an area. A still finer screen should be employed if a quantitative determination is desired.

While this report represents only the results of 5 samples from one type of substrate from one area, we can arrive at some approximation of effectiveness of previous quantitative surveys. A mesh size of 1.5 mm has been the most commonly used screen in the past, and Figure 1 shows that about 75% of the species would be recovered, but less than 10% of the specimens. A screen opening of 2.2 mm would naturally retain even smaller percentages. The mesh opening of 0.2 mm used by Moore (1931) would probably be extremely effective in obtaining all of the macroscopic species and the majority of the specimens. However, the time involved in analyzing such samples screened through an 0.2 mm mesh would be several times that of a mesh of 0.85 mm or 1.5 mm. It is not the purpose of this paper to recommend any particular screen size for use in future work, but rather to point out the importance of considering this variable when undertaking a quantitative survey of a marine area. The author has employed a size 20 screen (0.85 mm) in the majority of his studies of bays and harbors (Reish 1955), and Hartman (1955) has used a size 24 screen (0.7 mm) in her quantitative survey of San Pedro Basin, California.

Summary

1. The importance of the screen opening in washing marine quantitative samples was discussed. Five samples were washed separately through a series of 11 graded Tyler screens. The data were analyzed as to biomass, number of species, number of specimens, and the appearance and disappearance of the species.

2. Over 90% of the biomass, number of species and number of specimens were retained on screen size 12, 20, and 60, respectively.

3. The majority of the species appeared and disappeared by screen size 20.

4. The results were used to determine the effectiveness of previous marine quantitative surveys.

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A NOTE ON SOME MORTALITY FACTORS OF THE EUROPEAN CORN BORER, *Pyrausta nubilalis*[1]

Barber (1926) classified 26 physical and biotic factors which are responsible for the natural control of the European corn borer in New England. These factors are effective on different stages of this insect. This interesting work was justly cited by Allee *et al.* (1950) as a general case to illustrate the complexity of population dynamics. Barber, however, did not mention the host reaction as a factor. This omission is understandable since, according to Painter (1951) and Dicke (1955), the relationship between host conditions and the survival of borers was not recognized in this country until 1927 (Caffrey and Worthley 1927, Huber *et al.* 1928). Since then, the effects of the genetical and physiological conditions of the host plant on borer oviposition, larval survival, and larval development have been studied in a large number of varieties of corn.

Only a few authors actually analyzed the specific characteristics of the host plant which might be responsible for the borer mortality. Among these, Patch and Bottger (1935), in their study on the hybrid Hy × R4, observed that the upper leaves of the plant tend to enclose the tassel tightly until the plant is ready to shed its pollen. They felt that this characteristic prevents the easy access of borer larvae to the tassel, and is responsible for the reduced larval survival on this hybrid. Patch (1943) further showed that the delayed appearance of the tassel in this hybrid is also responsible for the low larval survival. Huber (1938) and Patch (1943) both obtained evidence that differences between hybrids occur during the time when the young larvae are feeding on the partly unfurled leaves. It may thus be inferred that some chemical or physical conditions of such leaves are responsible for the differential larval survival. Pepper and Garrison (1941) reported an interesting observation on New Jersey corn hybrid No. 2 on which the borer suffers a high mortality. They found that the wall of the stalk of this hybrid is harder than any of the 6 other strains studied. Recently, work was done by S. D. Beck and his associates on the chemical nature of resistance. This aspect has been adequately reviewed by Painter (1958).

During the various studies carried out in Minnesota in the past ten years on the ecology of the corn borer, many factors which affect borer survival were observed. Three factors which have not been previously reported will be discussed here.

1. *Larvae drowned in plant sap.* During their development the borer larvae feed on the inner surface of the leaf sheath and in the stalk. Usually no excess sap oozes out from the sites of these injuries. But on occa-

FIG. 1. A 4th instar larva drowned in the jelly in a lesion in leaf sheath. Note the lesion is filled with the jelly-like material.

FIG. 2. A 5th instar larva caught and pinched at the point of breakage of the tassel stalk.

[1] Paper No. 3941, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. The information reported in this paper was obtained when the author was working on the projects which are sponsored by the department of Entomology and Economic Zoology, University of Minnesota, St. Paul, Minnesota, and are under the leadership of Dr. F. G. Holdaway and Dr. A. C. Hodson.

FIG. 3. An adult trapped inside of the tunnel.

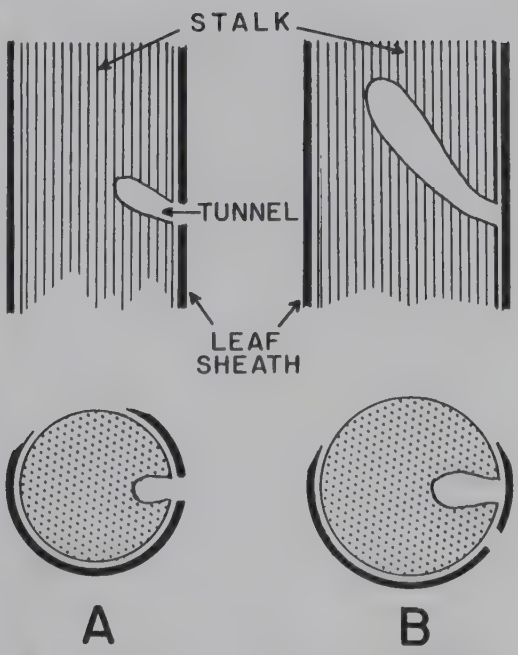

FIG. 4. A. Tunnel made through the sheath and into the stalk.

B. The stalk grew, and the hole on the sheath shifted its position. The tunnel is blocked.

sional plants, usually at a very succulent stage, the space between the sheath and the stalk, and the space within the tunnel in the stalk may be filled with plant sap which, at the time of dissection and observation, is in the form of a colorless and transparent jelly (Figure 1). Larvae have been noted drowned in this medium. Such larvae usually appeared pale, soft, and fully extended. Most of them were in the second, third and fourth instars, but a few fifth instar larvae have also been observed.

2. *Larvae caught at the point of breakage of the plant.* The tunnelling of the stalk by the borer larvae weakens the stalk. The stalk may break over at these weakened points due to the combination of the weight of the ear or tassel and strong winds. On a number of occasions, a larva was observed inside the tunnel right at the point of breakage (Figure 2). The larva was pinched and squeezed by the bend. Body contents of the larva were pushed toward the ends of the body, leaving the pinched point flat. The larva may or may not show any external wound. Larvae involved in this situation were usually in the fourth and fifth instars.

3. *Adult trapped in tunnel.* The borer larvae enter the stalk by chewing a hole on the side of the stalk. During the first generation, it is very common for larvae to make a tunnel and feed inside, but to leave the tunnel at the end of the feeding period and pupate on some exposed parts of the plant. Sometimes a larva may make the hole on the part of the stalk which is wrapped by the leaf sheath. In this case, the hole will be made through the sheath as well as the wall of the stalk. As the plant grows, the stalk becomes stouter. Since the leaf sheath does not grow correspondingly during that period, it shifts its position on the stalk as the stalk grows. As a result, the hole on the sheath gradually loses its alignment with the hole on the stalk, and eventually the hole on the stalk will be closed up by the sheath. When this happens, the borer inside the tunnel will be blocked from leaving the tunnel either as a larva or as a moth. On many occasions when the plant was dissected, a moth was seen inside the tunnel, very near the exit, dead, and with the wings still folded, as shown in Figure 3. The shift in the position of the sheath in respect to the stalk is diagramatically shown in Figure 4.

All the 3 mortality factors described were observed only incidentally during the dissection or while making other observations of the plants for a number of different studies. No systematic records were taken to evaluate quantitatively the importance of these factors in relation to host variety or season. Apparently these factors play only a minor role in the natural control of the insect. Of greater interest perhaps is the fact that these observations add to our literature some additional examples of the interactions of the borer and its host plant. First, the victim of each of these mortality factors are well preserved within the plant structures, and are definitely identifiable as to the cause of their death. Secondly, the mortality, particularly from factors 2 and 3, is inflicted on the borers by accidental changes in the host plant which are initiated by the activities of the borers themselves.

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PASSIVE OVERLAND TRANSPORT OF SMALL AQUATIC ORGANISMS

A preliminary study of various aspects of the passive overland dispersal of small aquatic organisms showed that a number of larger animals carry such organisms across dry land. This program is being continued in central Texas for comparison with and elaboration of the data here reported from the northeastern U.S.

The carrier animals were collected in the summer of 1956 in the region of Ithaca, N.Y. With the exception of a duck which flew from a pond and was then shot over dry land, no carrier animal was observed in contact with naturally occurring water. The feet and bills of birds were rinsed in sterile water. These birds had landed on dry soil or vegetation (with the exception of two crows which landed on snow surfaces) after being shot. Contamination may have occurred during this contact of the birds with the ground, but it seems unlikely that organisms picked up in this way would be very different either quantitatively or qualitatively from those picked up during the normal activities of the birds.

Table I. Organisms cultured from animals collected on land

	No. sampled	Unicellular algae	Filamentous algae	Illoricate Rodifers	Nematodes	Hypotrichs	Green flagellates	*Colpoda sp.*	Moss	Blank
Spring peeper	10	10	1	1	0	0	1	0	0	0
Black duck	1	1	1	1	1	0	0	0	0	0
Crow	6	6	4	1	1	0	0	0	0	0
Goldfinch	2	1	2	1	0	0	0	1	0	0
Song sparrow	1	0	1	1	0	0	0	0	0	0
Dragon fly	24	23	4	0	0	0	1	0	2	1
Damsel fly	6	6	2	0	0	0	0	0	1	0
Chironomid	9 (x5)*	3	0	0	0	0	0	0	0	6
Caddis fly	3	2	3	0	0	0	0	0	1	0
Crane fly	16	7	10†	0	0	0	1	0	9	0
Mosquito	5	0	1	0	0	0	0	0	1	4
Total	93	59	29	5	2	1	3	1	14	11

*Five flies were washed in each of these 9 cultures.
†Some of the indicated filamentous algae may have been moss protonema.

The frogs, which were all caught when they were sitting on teasel plants, could not have been contaminated during capture, as each was pushed into a sterile vial with the sterile surface of the cork from that vial. The same technique was used to capture the damsel flies, chironomids, caddis flies, crane flies, and mosquitos. Of these insects, all but the damsel flies were captured on a clean lighted sheet to which they were attracted at night. Control vials, which were moved against the sheet as if insects were being caught, were all negative (except for mold) when cultured for aquatic organisms.

The dragon flies were shot with a pistol and .22 shot cartridges. Only those animals which remained on the vegetation upon which they had been resting or which fell to undisturbed ground were used. They were transferred to sterile vials, again using the sterile surface of the vial's cork as the only tool. (The cork was of course not allowed to contact anything but the animal concerned.) While it is possible that insects dropping to the ground might become contaminated, such contamination if it occurred was of minor nature since the animals which did not fall to the ground produced cultures which were undistinguishable from those which landed on the ground.

Animals other than birds were soaked in sterile water for at least 12 hours and shaken with this water several times. The water was then cultured under constant light at 22°C. and examined periodically for about two months. Results are summarized in Table I.

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SOME REMARKS ON THE PERCOLATION OF LIGHT THROUGH THE FOREST CANOPY

In a forest stand the cover composed of tree leaves stretching over the earth's surface forms a forest canopy. It is obvious that the light permeability of this canopy is inversely proportional to the mass of leaves. The mass of leaves is defined by a relation which has been deduced by M. Czarnowski on the basis of some papers of W. R. Adams (*vide* Kittredge 1948), Kittredge (1948), and Achromejko (1949), namely: where

$$m_l = k\,(d + \Delta)^2$$

d = diameter breast high,
m_l = mass of leaves (dry weight),
k = constant for definite species and locality and biocenological conditions,
Δ = constant for definite species (for *Pinus silvestris* $\Delta = 1.7$ cm ≈ 0.67 in.).

TABLE I. Light percolation through the canopy in relation to the angle of incidence. (Sun disc below the angle from zenith 60°, cloudless sky)

α	$\cos\alpha$	$\frac{1}{\cos\alpha}$	$\frac{1}{\cos^2\alpha}$	$\frac{I}{I_0}$ per cent Experimental values.	$\log\frac{I}{I_0}$	$\frac{1}{\cos\alpha}\log\left(\frac{I}{I_0}\right)$	$\frac{I}{I_0}$ per cent. Values calculated by formula (3)
0	1,0000	1,000		38			38
5	0,9962	1,004					36,4
15	0,9659	1,035					32,9
25	0,9063	1,104	1,2188	26,6	1,4249	1,5741	26,5
35	0,8192	1,221	1,4908	19,1	1,2810	1,5641	18,3
45	0,7071	1,414	1,9994	9,1	0,9590	1,3560	10,0
55	0,5736	1,743	3,0380	3,6	0,5563	0,9696	3,5
		5,482	7,7470		4,2212	5,4628	

Thus there is a connection between light percolation of the forest canopy and basal area of a whole stand. Consequently the examination of light percolation of the forest canopy is of greatest practical importance, the more so as it makes it possible to define the wood volume in a forest stand by means of photo-electrical methods.

The authors of the present note came to the conclusion that the first thing to do is to find the connection between light percolation and the angle-length from the zenith. This is necessary because, if this phenomenon is not rightly understood, it is impossible to elaborate a correct method of finding the value of percolation as a mean value for a surface of 0.1 ha rank (or according to the U. S. customary system of 0.01 acre rank).

Thus the relation between the light percolation of the canopy and the angle-length from zenith (i.e. the distance covered by a light beam passing through the crowns) is surely a basic problem in forest ecology. It shows how the space is filled with the mass of leaves and how much light reaches the earth surface. As far as the present authors are informed, this problem has not yet been investigated.

OBJECTIVE

We limited our research to only one stand, namely to a twenty-five-year-old Scots pine (*Pinus silvestris* L.) stand in the forest of Białowieza (Poland). The stand in question had also the advantage of uniform density and crown contact.[1]

METHODS

The present writers applied a simple method—they measured the intensity of light descending from various zones, when the angles between the incident ray and the zenith were ascertained. The measurement was carried out simultaneously in the forest and in an open space not far away.

The photoelectric selenium cells Lange-Type S 60 were put in boxes of 1.15 × 1.15 × 0.50 metre size (= 3 ft. 10 in. × 3 ft. 10 in. × 1 ft. 5 in.). In the upper cover of the box, perfectly horizontally located, six concentric rings were cut out (Fig. 1). The sizes of the rings were matched so that after taking out the rings one by one, from the place of the location of the cell, the latter was exposed to these zones, respectively: from 0° to 10°, from 10° to 20°, from 20° to 30°, from 30° to 40°, from 40° to 50° and from 50° to 60°. We did not consider the more remote zones because of the technical difficulty of dealing with boxes bigger than those which we were using. Besides the more remote zones were of little use for our purposes. We measured the light percolation of the forest canopy *in zenith* in 270 spots (points) on the earth surface with the cell located at the bottom of a portable cylinder set perpendicularly (Fig. 2). The boxes with the

[1] Further data on this stand follow:

age a = 25 years,
height H = 11.0 m = 36 feet,
diameter d = 10.1 cm = 4.0 inches,
number of trees N = 3250 per ha = 1330 per acre,
basal area G = 26.25 m²/ha = 11.4 sq. feet/acre
locality: site class by Czarnowski N = 40, by Schwappach Bonität I.
density z = 1.0
stocking factor x = 0.7
Remarks:

$\left(\frac{\text{actual volume}}{\text{maximal volume}}\right)$ = stocking factor.

$\left(\frac{\text{actual number of trees per acre}}{\text{normal number of trees per acre}}\right)$ = density.

FIG. 1.

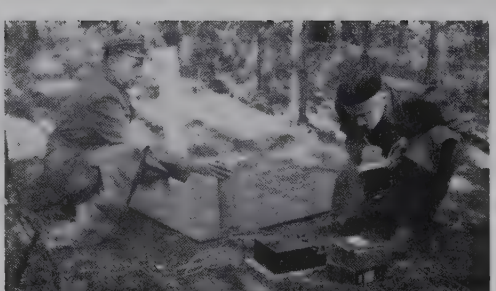

FIG. 2.

rings and the cylinder were black inside and were light-proof, but the sizes in comparison with the surface of the cell were so large that it was allowable to neglect the parallax. The cells had spectrum sensitivity similar to that of the human eye, thus being most sensitive in case of yellow-green. The electric current was measured by means of a galvanometer with the hand or with the mirror-and-scale. The dependence between the current and the light intensity was known. The measuring was made when the sky was clear and twice when the sky was quite covered with a uniform covering of clouds opaque to the sun-disc. In the first case the distribution of brightness on the sky depended on the situation of the sun-disc, while in the second case it did not (Kondrat'ev 1954, Piotrowski 1956). The simultaneous measurings of light intensity of the definite canopy zones (I) and of the intensity in the open space (I_o)—neglecting the influence of the light scattered in the tree-crowns—enabled us to define the light percolation of the canopy as a function of the angle of incidence of the light α, namely:

$$f(\alpha) = \frac{I}{I_o} \qquad (1)$$

We supposed that the function $f(\alpha)$ ought to be an exponential function of length, i.e. of the distance covered by the light in the tree-crowns, if, of course, a disturbance caused by different character of various beams of light which radiate from the canopy may be neglected. A paper by J. Słomka deals with that problem. Therefore we supposed that the nearest approximation of the function $f(\alpha)$ is a function of Bouguer-Lambert

$$f(\alpha) = \frac{I}{I_o} = b^{\frac{1}{\cos\alpha}} \qquad (2)$$

where "b" means a coefficient of percolation of canopy, and α is an angle of incidence of light. Further on we shall consider to what degree that approximation is true.

But we can easily see that if the formula (2) were valid, the term b would have the value from 0.1 to 0.02 for the different value of term α, therefore

$$b + \text{const.}$$

For that reason we conclude that the right formula for the distribution of the brightness transferred through the forest canopy is rather:

$$\frac{I}{I_o} = w \cdot k^{\frac{1}{\cos\alpha}} \qquad (3^1)$$

By the term $(w \cdot k)$ is meant *the zenith percolation* of a forest canopy. Its value indicates the mean percolation of a number of perpendicular parallel rays of light passing through the canopy. The measurements taken in our stand had the value 38.6%.

RESULTS

The measuring of the relative value of light intensity indicates that the values of the parameters according to the modified by us Lambert formula (3) and worked out by the method of the least squares, are

$$w \approx 9$$

$$k \approx 0.042$$

(Table included.)

It is worth taking into consideration that when we eliminated chance (casualty) of the position of the instrument in the stand by shading the cell from the zenith with a small screen, and when simultaneously we applied a very obtuse cone containing a large shred of the canopy, we could approximate with sufficient accuracy the value:

$$\text{When } 100 \cdot w \int_{\alpha_1}^{\alpha_2} k^{\frac{1}{\cos\alpha}} \, d\alpha \qquad (4)$$

$$k = 0.042$$

then

$$\int_{0^\circ}^{90^\circ} 0.042^{\frac{1}{\cos\alpha}} \, d\alpha \approx 1.7 \qquad (5)$$

(computed according to the Simpson formula).

In the examined pine-stand the ratio of the mean brightness under the canopy to the brightness in the open space was from 15 to 21% (measured in the cone from 20° to 60°) depending on the clouding of the sky.

As it has been proved by experiment, the most closed stands of Scots pine let pass through the canopy on an average from 11.2 to 13% of light in the open space

[1] Calculation of the values of terms w and k in the formula (3) using the experimental values:

$$\frac{7.747 \times 4.2212 - 5.482 \times 5.4628}{4 \times 7.747 - (5.482)^2} = \frac{+2.7546}{0.9357} = 2.9439 = \log(100w)$$

$$100w = 879$$

$$w \approx 9$$

$$\log k = \frac{4 \times 5.4628 - 5.482 \times 4.2212}{0.9357} = \frac{-1.2894}{0.9357} = -1.3780 = 0.6220 - 2$$

$$k = 0.0419 \approx 0.042^{\frac{1}{\cos\alpha}}$$

Then

$$\frac{I}{I_o} = w \cdot k = 9 \times 0.042^{\frac{1}{\cos\alpha}}$$

which is controlled in the last column.

(Oelkers, Czarnowski, Sacharov), therefore in order to obtain $k = 0.042$ and $w = 9$ the mean light percolation of canopy of a pine-stand with the stocking factor 0.7 ought to be

$$100 \times 9 \times \frac{1.7}{90} = 17\%$$

and in a most closed pine-stand: $17\% \times 0.7 \approx 12\%$.

In this way our results coincide with those obtained by other scientists.

The above considerations show that for expressing the distribution of light radiation passing through the forest canopy, formula (3) can be used.

Discussion

The electric current of a selenium photo-cell depends not only on the intensity of light, but also on its spectrum, angle of incidence and temperature. Influence of the temperature and of the angle of incidence of light can be neglected, but influence of the spectrum will be considered.

We supposed that the forest canopy makes the light weaker only in consequence of absorption. We did not take into consideration the light scattered in the crowns. It is very difficult to appreciate the influence of the scattered light and only approximate values can be obtained. Luckily we were able to cope with the problem thanks to favorable circumstances; namely, when the sky is slightly covered with small clouds of Cumulus humilis type, the light distribution on the sky changes very little within few minutes, except when a cloud covers the sun. When this begins, the total light intensity falls suddenly.

It is enough to make two measurements of intensity of the light falling from the particular region of canopy: first, when the canopy is lighted by the sun and sky light; second, when the canopy is lighted only by the sky light (when the disk of sun is veiled by cloud). The difference of values obtained from those measurements is just the intensity of sun light scattered in the canopy. Overlooking the influence of the angle of incidence and the influence of color of the light falling on the forest from outside, we can say that the intensity of light scattered in the canopy is in proper proportion to the sun light intensity measured over the forest. Knowing the coefficient of proportionality we can measure easily how much light (from the particular region we receive) is scattered by the leaves, and how much penetrates directly (through leaves and gaps) when forest is lighted only by the sky light. In this way we found that according to our measurements the participation of scattered light which passed through the crowns amounts at the most to 50%.

These results show that if we want to eliminate most of the scattered radiation, we must first eliminate the immediate sun radiation, and consequently we must measure the light intensity when the sky is clouded, or, when the sky is cloudless, the position of the sun disc must be near the horizon.

Now let us return to the question of the disturbance which arises from a change of spectrum in the forest in comparison with an open space. In the coniferous forest stands the change of spectrum arises as a result of light scattering in the pine-needles. The changes arising from a selective absorption are negligible. The maximum of radiation scattered by the needles falls on the spectrum ranges of green and yellow (Krinov), that is on ranges of maximal sensitivity of the photo-cells used. This covering of spectrum maxima was very difficult to deal with. More accurate data have been obtained using the filter, namely: 1) a blue filter (Schott BG 12) that seriously reduces the scattered radiation in the crowns, and 2) an orange filter (Schott OG 2) that allows only the yellow-green light to pass. The intensity difference between the measurements made with the first and the second filters indicates that the share of scattered radiation in tree-crowns ranges from 10 to 20%

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SULFUR DEFICIENCY IN SOILS FROM BRAZILIAN CAMPOS

The writers would like to describe briefly the results of some greenhouse studies which were undertaken as a step in determining the agricultural potential of several Brazilian campos but which may have some interesting implications to those concerned with the ecology of these areas. The term campo as used here refers to the upland savannas common to central Brazil as described by Bartlett (1956).

Data on possible soil fertility problems of several campos of the States of São Paulo and Goiás were reported recently (McClung, *et al.* 1957). These results, obtained from greenhouse pot culture studies, suggested that acute phosphorus deficiency might be the most important fertility problem common to the six soils studied. In five out of the six cases omission of phosphorus resulted in growth of grasses and legumes of only 10 to 15 per cent of that obtained with the complete fertilizer. Relatively small decreases in growth of grass occurred when nitgrogen was omitted. The omission of lime in certain instances resulted in decreased growth, but no significant differences in growth were measured when potassium was left out. In five out of the six soils studied growth was considerably diminished when the elements boron, copper, iron, zinc, moylbdenum and sul-

fur were omitted as a group. The purpose of this note is to present data indicative of the role of sulfur in this reduction in growth.

Three campos in the State of Goiás and one in São Paulo were sampled. The Goiás samples came from the vicinity of Anápolis. This region has recently received considerable attention since it is near the new Federal District of Brazil and hence may assume much more economic importance than it has enjoyed in the past. Feuer (1956) in an exploratory investigation considered this zone to be a multicyclic uplifted peneplane in which he designated three distinct erosion surfaces. Following his terminology one of the samples used here came from the oldest surface and two from the second. All three were in grass and light scrub savanna. At the sample sites the first erosion surface had a slope of about 2 per cent and the second 6 or 8 per cent. All three soils were Humic Latosols with clay loam "A" and clay "B" horizons. Only the "A" horizons were sampled for greenhouse study. The profiles contained no gravel in the surface two meters and there was no evidence of physical properties which might seriously impede water movement or plant root development.

The São Paulo sample (Soil "2") was obtained from a nearly level campo with somewhat heavier scrub vegetation than occurred at the Goiás sample sites. The soil was a sandy Latosol of the type classed as Terra Roxa misturada by Brazilian soil scientists.

All four soils had a pH of 4.8 to 5.2 with very low levels of acid extractable bases by the methods of Catani *et al.* (1955). Feuer's data for the Goiás region indicated the soils typically to have degrees of base saturation varying from 1.0 to 15.0 per cent using the ammonium acetate extraction procedures. Although these determinations were not made in the present project the data suggest that the soils probably fell in this general range.

The Goiás region has a mean annual rainfall of about 65 inches with a distinct dry season during the winter months. Elevation is about 3,000 feet and mean annual temperature 70°F. The São Paulo sample site was about 500 miles farther south and at a somewhat lower elevation. Seasonal variation in temperature is consequently greater but mean annual temperature about the same. Rainfall is slightly lower than in Goiás with a distinct but shorter dry season.

Pot culture tests were carried out in which alfalfa and Italian ryegrass served as the indicator crops. The general plan of the experiment was to apply most of the essential plant nutrients in a "complete" treatment and to compare growth with that obtained when one or more of the elements were omitted. In addition to the elements listed in Table I the complete treatment for alfalfa included pH adjustment to 6.0 with $Ca(OH)_2$ and $MgCO_3$ and liberal application of phosphorus and potassium as KH_2PO_4. The complete treatment for ryegrass included in addition a substantial level of nitrogen applied as NH_4NO_3. Molybdenum was applied as NH_4MoO_4, boron as borax, sulfur as calcium sulfate and the heavy metals as ethylene diamine tetraecetic acid chelates. Calcium chloride was added to provide an equivalent amount of calcium on the treatments from which calcium sulfate was omitted.

The dry matter production data given in Tables I and II indicate that the depressions in growth noted on these soils were due almost entirely to the omission of sulfur. Leaving out molybdenum had an adverse effect (.05 level), on growth of alfalfa (Soil "2") but not on ryegrass (Soil "1"). Yields of alfalfa on a number of treatments with one micro nutrient omitted were considerably above

Table I. Effects of sulfur and micro nutrients on growth of rye-grass and alfalfa on soils from two Brazilian campos

Treatment	Dry Weight of Tops (gm. per pot)	
	Soil "1" (Goiás) Ryegrass	Soil "2" (São Paulo) Alfalfa
"Complete"	10.4	11.9
Minus Mo	11.5	9.4
Minus Cu	10.8	15.4
Minus Zn	12.3	14.9
Minus Fe	12.1	18.0
Minus B	12.0	16.3
Minus S	1.4	3.9
Minus Mo, Cu, Zn, Fe, B and S	0.6	4.3
L.S.D. (.05)	2.01	2.12
(.01)	2.92	2.94

Table II. Effects of sulfur and micro nutrients on growth of rye-grass on campo soils from Goiás

Treatment	Dry Weight (gm. per pot)	
	Soil "3"	Soil "4"
N, P, K, S, Mo, Zn, Cu, Fe, B	11.5	14.5
N, P, K, S, Mo	10.4	14.0
N, P, K, S	10.6	13.9
N, P, K, Mo	0.4	2.7
L.S.D. (.05)	1.08	1.34
(.01)	1.63	1.90

the complete treatment. These differences were significant at the .01 level. Further work is needed to explain this response.

The generally low fertility of soils of Brazilian campos has long been recognized and the low levels of base saturation, low organic matter content and poor phosphorus status have been pointed out (Feuer 1956, Paiva Neto, *et al.*, 1951). To the knowledge of the authors the existence of an inadequate sulfur supply has not been reported. According to the data obtained thus far sulfur is of importance second only to phosphorus as a nutritional factor affecting growth of grasses. (It should be emphasized that in no case have responses been obtained to sulfur unless phosphorus was also applied.) Although the major bases are present in poor supply they are not immediately limiting. For the legumes tested this was not necessarily true, for growth was extremely poor when lime was not applied. Determination of the true agronomic importance of these findings must await testing on a field basis. Qualitatively, however, they are probably valid estimates of the fertility status of these soils. It should be stated, incidentally, that in the opinion of the authors the soil physical properties of many of the campos are satisfactory for much more agricultural development than is generally supposed. Feuer (1956), in his study of soils in Goiás, has previously expressed a similar view.

A number of writers (cited in Bartlett 1956) have postulated fire as the predominant factor in determining the climax vegetation of the campos. Edaphic factors may or may not have played an important role in their

development. It is difficult to believe, however, that the acute deficiencies noted above would not at some point affect the natural vegetation of these areas. Should their nutrient status be altered to alleviate these deficiencies, some change in botanical composition seems likely. Perhaps the changes would be of minor nature if periodic burning continued. Conversely, however, cessation of burning might have a relatively small effect if nutrient status remained unchanged.

The possibility that these examples of sulfur deficiency are related to losses of sulfur from the campo due to repeated burning is an interesting line of conjecture. The authors have obtained data indicating that some seventy-five per cent of the sulfur contained in dry grass is volatilized during burning under simulated field conditions. This, coupled with the fact that sulfur in the plant ash is more susceptible to loss through leaching, could explain a very poor sulfur status.

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A RECORD OF REVERSE PLANT SUCCESSION IN A TAMARACK BOG

Introduction

This paper reports on a series of records which document what appears to be a clear-cut case of reverse plant succession, and discusses the probable cause of this phenomenon.

General notes made on the vegetation of a tamarack (*Larix laricina*) bog by the class in vertebrate ecology at the University of Minnesota Forestry and Biological Station during the summers of 1946 through 1954 resulted in observations of pronounced changes in the species present and cover conditions. W. H. Marshall and M. F. Buell of the station staff made certain records between 1952 and 1956. The study reported here records detailed data obtained in 1957, reviews the notes of past years, and considers the most probable developmental and environmental causal influences.

The study area was located in Section 1, T. 143 N., R. 36 W. along the upper bog area of Floating Bog Bay Creek in Itasca State Park, Minnesota. The specific area studied in 1957 was 36 × 48 yards. It included a fourth-acre plot studied by the ecology classes of 1946 and 1947, and also part of the one-acre plot used by the classes from 1948 to 1954.

Methods

The classes in 1946 and 1947 gave a brief description and listing of the principal plant species and made detailed maps of the tree, hummock and pool locations on the one-quarter acre area. In 1952 the one-acre area, including the previously studied one-quarter acre, was examined in detail and a species list was compiled by Drs. Marshall and Buell. Quantitative data were not collected in any of these years, but the changes were pronounced.

In the summer of 1957 the herbaceous vegetation of the study area was sampled using 48 pairs of one square meter quadrats distributed in a checkerboard fashion. One of each pair was located on a hummock and one in an adjacent hollow. The frequency of a species was determined by its occurrence, expressed in per cent, in the 48 hummock and hollow quadrats respectively. Similarly, cover of a species was expressed as the average estimated per cent for each of the 48 hummock and hollow quadrats respectively.

Nomenclature is according to Gray's Manual of Botany, 8th Ed. (Fernald 1950). Voucher specimens are on file in the Herbarium of the University of Minnesota.

Results

The canopy was dense in 1946. Based on extrapolation of the numbers of living trees accurately mapped in the quarter-acre plot in 1946, there were 1,904 trees per acre in this stand at that time. These were all tamaracks 30 to 40 feet in height and 2-4 inches d.b.h. By 1952 many of the smaller trees had died and ten of the larger trees had fallen in the one-acre study area. In 1957, there were 1,806 trees standing per acre, 886 of which were dead. In addition, there were 335 fallen trees per acre, 78 of which were moss covered indicating they had been lying on the ground much longer than the other fallen trees.

The death of the tamaracks opened the canopy considerably. This was evident from the aerial photographs of the area taken in 1939, 1949, and 1951. The canopy appeared as a solid, velvet-like mat in the 1939 photographs. It appeared somewhat irregular in the 1949 photographs and several openings were evident in the 1951 photographs.

The appearance of the ground in 1946 was of an almost bare uneven surface with small dark-colored pools and hummocks covered with red-brown tamarack leaves and some mosses.

The most abundant green plants at the ground level in 1947 were mosses that grew on hummocks around the tamarack trunks. Of the fourteen vascular plants listed only one sedge (*Carex disperma*) occurred sparingly throughout the area. Other plants noted as scarce were:

Bidens coronata
Caltha palustris
Cicuta bulbifera
Circaea alpina
Dirca palustris
Dryopteris thelypteris var. *pubescens*
Equisetum sp.
Ledum groenlandicum
Menyanthes trifoliata
Rubus idaeus
Sanicula marilandica
Scutellaria lateriflora
Viola pallens

By 1952, striking changes in the flora had taken place giving the surface a definitely marshy and herbaceous appearance. At this time fifteen additional species of vascular plants were recorded. Wild calla (*Calla palustris*) grew profusely in the pools. A sedge (*Carex pseudo-cyperus*), cat-tail (*Typha latifolia*) and duckweed (*Lemna minor*) were all common in the depressions not dominated by wild calla. The pussy-willow (*Salix discolor*) had also invaded. Other plants which had appeared probably in response to the increased light are as follows:

Calmagrostis canadensis
Campanula aparinoides
Epilobium glandulosum var. *adenocaulon*
Galium trifidum
Glyceria striata
Habenaria hyperborea
Linnaea borealis var. *americana*
Muhlenbergia racemosa
Potentilla norvegica
Potentilla palustris

In 1957 the canopy was quite open with dead trees, both standing and fallen, as major components of the habitat. A considerable amount of light reached the densely occupied herbaceous level which contained 65 vascular plant species (Table I). Forty-two species had not been noted prior to 1957 while 6 of those recorded in either 1952 or 1947 were not found in 1957. Thus, there was a great increase in the species composition with relatively few deletions.

Certain plant species occurred in both hummock and hollow habitats, whereas others occurred in only one of the habitats. The delineation between the hummock and hollow habitat was difficult to determine with precision as it fluctuated with the rainfall, yet the appearance of each habitat was strikingly different. Twenty-one of the 53 plant species which occurred in the 96 study quadrats were restricted to the hummock habitat and two species were found only in the hollow habitat. Twelve species were found in the study area but did not occur in the quadrats (Table I). No record was kept as to the type of habitat they occupied.

In addition to the vascular plants, two genera of mosses were especially common; *Sphagnum* on the hummocks and *Mnium* on the periphery of the hummocks just above the water level. Although the frequency percent of *Sphagnum* was high in both habitats, its contribution to the cover was much greater in the hummock habitat (Fig. 1).

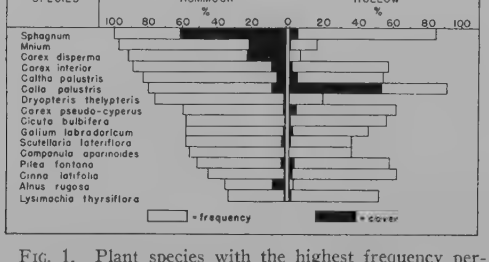

FIG. 1. Plant species with the highest frequency percentages in either hummock or hollow habitats and their respective cover percentages.

TABLE I. Vascular plants growing in the study area in 1957 with their frequency and cover percentages for hummock and hollow habitats. Species without entry in any of the columns were those found in the study area but not in the quadrats

	% FREQUENCY		% COVER	
	hummock	hollow	hummock	hollow
Agrostis hyemalis	13	13	< 1	< 1
Alnus rugosa	35	2	10	< 1
Aster junciformis	48	15	2	< 1
Aster puniceus	2	2	< 1	< 1
Betula pumila	6	0	1	0
Calla palustris	81	92	8	54
Caltha palustris	83	54	5	5
Campanula aparinoides	56	35	1	< 1
Carex aquatilis	6	17	< 1	1
Carex disperma	92	6	22	< 1
Carex interior	89	58	9	1
Carex paupercula	10	0	< 1	0
Carex pseudo-cyperus	60	62	1	4
Carex stipata	2	17	< 1	1
Cicuta bulbifera	58	56	1	1
Cinna latifolia	46	62	1	1
Circaea alpina	8	0	1	0
Cirsium muticum				
Corallorhiza trifida	4	0	< 1	0
Cornus canadensis	4	0	< 1	0
Cornus stolonifera				
Dryopteris spinulosa	6	0	1	0
Dryopteris thelypteris	77	19	1	< 1
Epilobium glandulosum var. *adenocaulon*				
Epilobium palustre	21	17	< 1	< 1
Equisetum fluviatile	2	13	< 1	< 1
Fragaria vesca	29	0	1	0
Galium trifidum	58	46	1	2
Galium triflorum	27	2	< 1	< 1
Geum aleppicum var. *strictum*				
Glyceria striata	19	33	1	2
Iris versicolor				
Larix laricina	6	0	< 1	0
Ledum groenlandicum	2	0	< 1	0
Linnaea borealis	2	0	< 1	0
Lonicera villosa	2	0	< 1	0
Lycopus uniflorus				
Lysimachia thyrsiflora	33	52	1	1
Mentha arvensis	4	0	< 1	0
Menyanthes trifoliata	4	15	< 1	1
Picea mariana	27	0	< 1	0
Pilea fontana	52	58	3	3
Pinus strobus	4	0	< 1	0
Poa wolfii				
Populus tremuloides	2	0	< 1	0
Potentilla norvegica	2	4	< 1	< 1
Potentilla palustris	15	19	1	1
Pyrola asarifolia	33	0	1	0
Ribes glandulosum	6	0	< 1	0
Rubus idaeus var. *strigosus*	4	0	< 1	0
Rubus pubescens	42	2	2	< 1
Rumex orbiculatus				
Salix discolor	8	0	< 1	0
Salix pedicellaris				
Saxifraga pensylvanica	8	2	< 1	< 1
Scutellaria epilobiifolia	29	42	< 1	1
Scutellaria lateriflora	58	35	2	1
Solidago canadensis				
Stellaria longifolia	21	29	< 1	< 1
Typha latifolia	0	10	0	< 1
Urtica gracilis	0	2	0	< 1
Vaccinium angustifolium	4	0	1	0
Vaccinium myrtilloides				
Vaccinium oxycoccus	4	0	< 1	0
Viola pallens				
Unknown	31	23	1	< 1

This lack of correlation between frequency and cover percentages was also noted in the vascular plants. The frequency of occurrence of *Calla palustris* was very similar in both habitats, whereas its cover percentage was much higher in the hollow habitat. *Carex disperma* and *Alnus rugosa,* however, were more restricted to the hummock habitat and comprised a goodly share of its cover (Fig. 1).

Many of the other species, although their frequencies were quite high, had low cover percentages. Forty-two of the 51 species found in the hummock study quadrats had cover percentages of 1% or less and a total cover percentage of 18; whereas only five species had cover percentages of 5% or greater and a total of 54%. Twenty-six of the 32 species found in the hollow study quadrats had individual cover percentages of 1% or less and a total cover percentage of 13; while three species had cover percentages of 4% or greater and a total of 63%. There was a great percent cover in the hummock than in the hollow quadrats; 163% in the hummock and 86% in the hollow quadrats. The high percentage is due in part to overlap of individuals.

Determination of acidity on July 14, 1957 showed the pH of the hummocks to be 4.2-4.5. Well within the hummoc' s below the sphagnum layer and in the hollows, the pH was 5.0-5.5. This is similar to results obtained by Conway (1949) working in bogs of this same area who found the hummocks to be more acid.

Environmental changes that seem to be related to the vegetation changes have been recorded. Surface water has increased during the ten years of observation. The class project report of Aug. 5, 1946, stated that "a hole about 6-8 inches deep readily filled with seeping underground water." The report of July 1948 stated that one or two inches of water often covered the area between the hummocks and the tamarack roots. The report of July 1952 stated that in 1949 and 1950 the water was 10-14 inches deep, and that it had remained the same, or had become deeper during the next two years. It is, of course, difficult to delineate the bottom of the standing water as the bog was quite soft where under water. The report of 1953 stated that the water was 18-24 inches deep, and in 1957 one sank to above his knees while wading through the area. Although some of these water depth figures are for August and some for July, the changes are in keeping with the general trend of water level in the Itasca Park area during this period.

An increase in hollow area was associated with the increase in water depth. The hollows were estimated as covering about 30% of the ground level in 1946-48, about 60% by 1953 and 73% by 1957.

The precipitation data at Itasca Park date from 1911. They show a general increase in precipitation since the early 1940's (Fig. 2). The much longer record, dating from 1888, at the Winnibigoshish Dam weather station fifty miles northeast of Itasca, shows a period of above normal precipitation in the early 1900's as well as since 1940 (Fig. 2).

Examination of growth rings from increment borings and cross sections of trees showed two periods of slow growth and two of rapid growth. Presuming that each ring represents a years' growth, the earliest group of narrow annual growth rings was formed approximately between 1902 and 1915 and the later group from the early 1940's to the present (Fig. 3). The observed increase of the ground water table in the study area during the last ten years coincides with the latter period of narrow growth rings, and the above normal precipitation in the Lake Itasca region appears to have been the cause of this increase (Fig. 2). The precipitation data at Lake

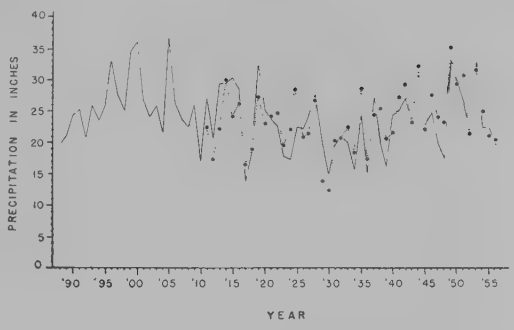

FIG. 2. Annual precipitation data for Winnibigoshish Dam and Lake Itasca Weather Stations.

Itasca and Winnibigoshish Dam from 1911 through 1956 have a correlation coefficient of .79. There is therefore good reason to believe that above normal precipitation also occurred at Lake Itasca in the early 1900's, causing an increase in ground water level and the consequent period of narrow growth rings.

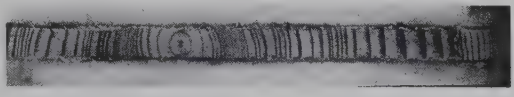

FIG. 3. Increment boring taken from a living tamarack in 1957 showing periods of rapid growth and slow growth. The first group of narrow growth rings was formed in the early 1900's and the later group dates from the early 1940's and continues to the time of sampling.

DISCUSSION

The increase of species in 1957 is probably the result of the changed environmental conditions of which the water level and light penetration to the bog surface seem to be paramount.

The pronounced rise in the water table and the resulting increase in surface water observed during the last ten years has been detrimental to the tamarack trees in this bog resulting in the death of many and the reduced growth of others. The small growth rings since the early 1940's and those between 1902 and 1915 (Fig. 3) were formed during periods of generally above normal rainfall (Fig. 2).

On the other hand, it appears that the large annual growth rings preceding the 1900's and during the 1930's reflect periods of favorable growing conditions. These two groups of rings correspond closely to periods of below normal annual precipitation (Figs. 2 and 3).

The recent death of the tamaracks resulted in a much more open canopy allowing more light to reach the lower levels. It is probably this factor that has been chiefly responsible for the increase of herbaceous species since 1947. The great increase of tree and shrub species is especially noteworthy, *Salix discolor* being the only shrub species recorded by 1952. All thirteen of the woody species observed in the quadrats in 1957 occurred almost exclusively on the hummocks. The scarcity of tamarack seedlings in the study area is probably due to the high water table (Duncan 1954).

The present trend of change in vegetation in the study area, if continued, will result in a shrubby and herbaceous undergrowth with a discontinuous overstory of tamarack trees.

SUMMARY

1. Decreased rate of growth and the increased mortality of the tamaracks appear to be related to the rise in water level caused by the increased precipitation since the early 1940's.

2. Pronounced increase in the herbaceous and shrubby vegetation of both hummocks and hollows accompanied the change of the tamarack canopy and the rise in the water level.

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ESTABLISHMENT OF A PERMANENT VEGETATIONAL TRANSECT ABOVE TIMBERLINE ON MT. MARCY, NEW YORK[1]

The field work entailed in the establishment of a permanent vegetational transect above timberline on Mt. Marcy, New York was performed during the last week of August and the first week of September, 1957.

This reference transect was placed during the course of an extended investigation of timberlines in general for the purpose of allowing future investigators to determine whether timberlines in the eastern United States are ascending or descending. The field investigation was carried out by a party of four[2] under the guidance of the author and entailed the back-packing of supplies and equipment totaling 110 pounds each to the top of the mountain, which is the highest point in New York State.

Earlier works (Adams et al., 1920), which inspired this investigation, were found to be inadequate for quantitative comparisons since no actual transects of any kind were made and information concerning exact locations was lacking in most instances.

It was felt that the portion of the investigation concerning the permanent transect was of sufficient importance to be reported separately. In order to remedy the earlier errors of not compiling sufficient information for comparative purposes, extreme care was taken in recording exact positions.

LOCATION OF THE BENCH MARKS

In order to correlate timberline with elevation it was necessary to place accurate bench marks closer to the study areas than the Coast and Geodetic Survey mark at the top. Two new bench marks were located on the northeast and southwest slopes respectively as close to the 5,000 foot contour as possible.

Although there is apparently some doubt at the present time concerning the accuracy of the recorded elevation of the Adirondack peaks, the assumption is made that the Geodetic Survey mark at the top of Mt. Marcy is 5,344 feet above mean sea level.

Since the tops of high mountains are subjected to sudden shifts of air movement and pressure areas, it is virtually impossible to set an altimeter at any one known point with the view of locating new bench marks accurately any distance away. In the matter of minutes the apparent elevation of any one point may change ten or even hundreds of feet, necessitating instantaneous correction between the two points.

Since the new bench marks at the 5,000 foot contour were in complete defilade and considerable ground distance from the mark at the peak, small radios were used to insure accuracy.

The U. S. Army Engineer Corps altimeters which were used during this study could be read with accuracy to the closest foot. In order to insure accurate placement of new bench marks, it was necessary to follow a rather strict procedure. At the 5,344 peak elevation the instruments were correlated by the small adjustment screws until both read exactly the same despite the fact that they did not record the true elevation at that time. The correction factor was recorded. One instrument was left at the peak bench mark and the other carried carefully to a prominent spot in the landscape 344 feet lower in elevation or as close to this figure as possible. The apparent changes in elevation at the top caused by vagaries in the air pressure were reported to the new bench mark by means of U. S. Army Handy-Talky Radios supplied by the Middlebury College R.O.T.C. Unit, allowing instantaneous correction.

Timberline-Bench-Mark-East (TLBM-E) is located approximately on the 45° azimuth from the top. It is at the elevation of 5,029 feet atop a prominent bedrock outcropping just south of the trail ascending the northeast slope of the mountain just as it emerges from the treeline.

Timberline-Bench-Mark-West (TLBM-W) is located approximately on the 245° azimuth from the peak in the general direction of Gray Peak, which is prominent in the very near distance to the southwest. It is at an elevation of 5,012 feet atop a tremendous boulder which is very evident as one descends Mt. Marcy in the direction of Gray Peak.

Bench marks and transect markers placed in the survey were steel eyebolts such as are used in quarrying operations for anchoring cables. The base of the stem of the eyebolt is split to receive a wedge which spreads and anchors the bolt when pounded into a previously drilled hole in the rock.

Once these new, more convenient, bench marks were located our further studies of timberline could easily be correlated with elevation.

Placement of the transect points is indicated in Table I and Figure 1.

TABLE I. Data for location of transect points.

Point of Departure	*Azimuth*	*Distance*	*Point Reached*
TLBM-West	203°	100 ft.	Transect Point #1
Transect Point #1	185°	100 ft.	Transect Point #2
Transect Point #2	305°	100 ft.	Transect Point #3
Transect Point #3	65°	100 ft.	Transect Point #1

[1] The author wishes to thank the DuPont de Nemours Corporation which furnished the funds necessary for the investigation, Dr. Stanley Smith and Dr. W. T. Winne who established the identity of the plants reported.

[2] Members of the party were: Mr. Donald Brightman, Mr. David Murray, Mr. Joseph Widli and the writer.

The three transect points are all on bedrock and are marked by the previously described eyebolts. Transect point #3 may be difficult to locate visually without following azimuth and distance since it is at present under the cover of black spruce branches.

All azimuth readings are referred to true north corrected from a magnetic north declination of 14°.

Elevations of the bench marks and transect points referred to in this paper are as follows:

Bench mark, Top	5,344 ft.
Bench mark, West	5,012 ft.
Bench mark, East	5,029 ft.
Transect Point #1	4,984 ft.
Transect Point #2	4,978 ft.
Transect Point #3	4,958 ft.

Description of Vegetational Transect

Location of the vegetational transect as close as possible to timberline in the alpine zone insures the quickest possible reflection of climatic change. Using TLBM-W as a reference point the triangular, 300 foot transect was laid out (Fig. 1). Distances recorded are ground distances obtained by stretching the steel tape from one point to another on the ground realizing that while horizontal distances would be more accurate they would be more difficult to obtain both at the time of this survey and in the future when the transect is reviewed.

Fig. 1. Ground plan of the permanent line transect.

The use of eyebolts to mark out the transect facilitated the stretching of the steel tape used in the survey. The vegetation was sampled by means of the line-interception method. Each plant touched by the line was recorded together with its interception to the closest inch. In a few instances the nanophanerophytes (dwarfed trees are included in this classification by Adams et al., since at this altitude they never assume phanerophytic form) overtop the "understory" of mosses, and small Vaccinium species especially. When this happened the vertical projection on the line of the dominant, covering plant was recorded and plants thus "covered" in the understory were not. Whether or not this decision was correct should make no difference provided future investigators record the transect in the same manner.

The three 100 foot legs of the triangular transect were treated as if they were a single 300 foot transect as far as analysis was concerned. The triangular form was felt necessary for two reasons: (1) the alpine meadows close to timberline are small and preclude the use of a single, straight transect of the length necessary to give reliable results, and (2) once two points were established the position of the third point was determined but unknown until measured preventing possible prejudice in the sample as far as possible.

Table II lists the plants recorded along the transect together with the total coverage in inches and the percentage ground cover each contributed. It should be noted that bare soil and bare rock are included in this list since they are an integral part of alpine landscape.

Table II. Interception data for plants encountered along the line transect

	Total Inches	% Total Cover
SPHAGNACEAE		
Sphagnum pylaesii Brid.	25	0.69
Sphagnum papillosum Lindb.	80	2.22
ANDREAEACEAE		
Andreaea rupestris Hedw.	42	1.16
GRIMMIACEAE		
Rhacomitrium heterostichum (Hedw.) Brid.	55	1.53
LYCOPODIACEAE		
Lycopodium Selago L.	7	0.19
Lycopodium annotinum L. var. *pungens* Desv.	5	0.14
PINACEAE		
Picea mariana (Mill) BSP.	280	7.77
Abies balsamea (L.) Mill.	210	5.83
CYPERACEAE		
Carex rigida Good. var *Bigelowii* (Torr.) Tuckerm.	9	0.25
Scirpus caespitosus L. var *austriacus*	290	8.05
BETULACEAE		
Betula alba L. var *cordifolia* (Regel.) Fernald	41	1.14
Alnus crispa (Ait.) Pursh.	11	0.31
CARYOPHYLLACEAE		
Arenaria groenlandica (Retz.) Spreng.	7	0.19
ROSACEAE		
Potentilla tridentata Ait.	67	1.86
EMPETRACEAE		
Empetrum nigrum L.	85	2.36
CORNACEAE		
Cornus canadensis L.	6	0.17
ERICACEAE		
Vaccinium uliginosum L.	1241	34.47
Vaccinium Oxycoccos L.	5	0.14
Kalmia polifolia Wang.	16	0.44
Ledum groenlandicum Oeder.	110	3.06
Chamaedaphne calyculata (L.) Moench.	18	0.50
DIAPENSIACEAE		
Diapensia lapponica L.	78	2.16
BARE SOIL	93	2.58
BARE ROCK	706	19.61
	3600	99.96

Results

Frequency figures were impossible to obtain since the individual plants could not be separated from the mat they produced in many instances. Cover appears to be the most reliable and indicative of all the ecological attributes and hence is the form in which the results are reported here.

All plants found and reported in this study were also reported by Peck (1899) and Adams *et al.* (1920). Of the plants found on the transect only four can be considered as non-arctic: *Cornus canadensis* L., *Abies balsamea* (L.) Mill., *Betula alba* L. var. *cordifolia* (Regel.) Fernald and *Carex rigida* Good. var. *Bigelowii* (Torr.) Tuckerm. (of which the type species is considered more northerly and the variety found only in the mountains of New England). On this basis the percentage of non-arctic plants totals 7.66%.

Future investigators should note any change in arctic versus non-arctic percentages and evaluate the invasion or loss of species on the transect. It is suggested that periodic checks be made every 10 years for, while no great change can be expected in this length of time, a trend established by three or four analyses would be of greater importance than a single analysis spanning a greater time period which could conceivably be affected by a single catastrophic climatic or erosional disturbance.

SUMMARY

An expedition to study timberline was undertaken in the late summer of 1957 to Mount Marcy, N. Y. During this time a permanent vegetational line-transect was placed just above timberline where climatic changes are most likely to be reflected in the future. Every effort was made to insure permanence and accuracy of the transect with a view to future comparisons. Plants encountered on the transect are reported as percent total cover. Non-arctic plants are reported as making up 7.66 percent of the vegetation in 1957.

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USE OF AN AERATED REFERENCE SAMPLE WHEN MEASURING DISSOLVED CARBON DIOXIDE

The importance of carbon dioxide as a raw material used in photosynthesis by aquatic plants is well known, but the problems associated with determination of CO_2 concentration in natural waters are not solved efficiently in any of the limnologic literature that I have studied. For example, the tenth edition of STANDARD METHODS FOR WATER ANALYSIS (1955) recommends the use of nomographs but warns that the user must determine the reliability of their application to specific waters. I have shown (Verduin 1956) that errors of 30 to 250 per cent are encountered when using Dye's (1944) nomographs to estimate CO_2 change in natural waters, and have recommended differential titration as used by Moberg, et al. (1934) for determining the relationship between pH and CO_2 change in natural waters. The titration of measured volumes of water with weak NaOH to the phenolphthalein end-point has long been used as an approximate measure of free carbon dioxide but the end-point is found at widely variant pH values in different waters, and does not coincide with the disappearance of carbonic acid (see the C_2 column in Table I). The Van Slyke and the Henderson-Haldane apparatus have been used for determination of free carbon dioxide (Moberg, et al., 1934, Loomis, 1957) but a method requiring less cumbersome and expensive equipment is needed for a determination that is of such wide application in studies of aquatic ecology. Loomis has postulated that high free carbon dioxide concentration may be the stimulus which initiates sexual stages in many aquatic organisms. His hypothesis cannot be tested conveniently unless a simple method of determining free carbon dioxide concentration is available. I will now describe such a method.

Because the phenolphthalein color change does not take place at the end of the free carbon dioxide titration, but is influenced by the presence of other dissolved substances, we need a reference value which can be used to correct the titration value. Such a reference can be obtained easily by collecting a duplicate water sample and aerating it thoroughly. This can be accomplished by pouring it into a shallow dish (water depth of less than one-half cm) and allowing it to stand exposed to the atmosphere for about four hours, or by pouring it into a finger bowl and stirring vigorously for an hour or more, either with a mechanical stirring device, or an aquarium aerator. After this treatment the water can be assumed to have a free carbon dioxide content close to equilibrium with the atmosphere. If the air to which the water was exposed is not seriously contaminated by products of respiration or combustion (the air in a well-ventilated room usually meets these requirements) its carbon dioxide content will be 0.6 mg/liter or 13.6 μmoles per liter. The solubility coefficient of carbon dioxide in water at various temperatures (1.7 at 0°C, 1.2 at 10, 0.88 at 20, 0.66 at 30) can be used to obtain an estimate of free carbon dioxide concentration, in the reference sample, that is sufficiently accurate for ecological studies.

The true CO_2 concentration (C) is computed as follows:

$$C = C_1 - [C_2 - (C_3 \cdot S_t)]$$

Where C_1 is the free CO_2 concentration of the sample as determined by titration.

C_2 is the free CO_2 concentration of the aerated sample as determined by titration.

C_3 is the CO_2 concentration in the atmosphere and

S_t is the solubility coefficient at the temperature of the aerated sample.

(C_3 must be expressed in the same units as C_1 and C_2) Table I presents sample data.

The most interesting statistic in the table is C_2, the CO_2 concentration indicated by titration of the aerated sample. The value ranged from 39 μmoles/liter in distilled water, to 192 in sea water. And Urschel's Quarry water, which had a pH of 8.42 when in equilibrium with the atmosphere, showed a phenolphthalein color change at a pH of 8.09, when there were still about 130 μmoles of free CO_2 present. Negative values of this kind can

TABLE I. Corrected determination of free carbon dioxide in water, at 25°C. All values are μmoles per liter.* The value of C_3 is 13.6 and of S_t is 0.76, their product, 10 μmoles per liter, is subtracted from C_2 to provide the correction applied to C_1 to obtain the true concentration (C). All samples were aspirated to charge them with CO_2.

Sample	C_1	C_2	C
Distilled water	176	39	147
Tap water	310	60	260
Sea water	862	192	680
Urschel's Quarry water	223	−120	353

*To convert to mg/liter (ppm) multiply by 0.044.
To convert to ml/liter multiply by 0.0224.

be measured by titration with standard acid to the colorless phenolphthalein end-point. This titration is called phenolphthalein alkalinity by limnologists (Welch 1948) and is interpreted as an index of carbonate concentration. The negative value of C_2 in Table I shows how widely erroneous this interpretation may be on occasion. The use of an aerated sample as a reference in the determination of carbonate carbon dioxide would also improve the accuracy of that determination, especially in waters, like the Urschel's Quarry sample, which turn phenolphthalein pink in the presence of free carbon dioxide. If titrations for carbonate and free CO_2 are made using a pH meter to determine the end-point, an aerated sample also proves to be a most valuable reference point, indicating the pH value associated with a known, small, concentration of free carbon dioxide.

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A PUNCH CARD TECHNIQUE FOR STUDYING SPECIES AND SPECIES-ENVIRONMENT ASSOCIATIONS[1]

In studies of species associations across gradients of environment, it is necessary that sampling data be recorded so as to permit all quadrat records to be sorted for any combination of two or more species or for any recorded environmental conditions. A modified punch card system has been developed in which a manual sorting technique enables the investigator to do this with reasonable speed. As far as the authors are aware, no similar system has been described. Since it has application to many other kinds of community studies the technique and equipment are described below.

The Royal McBee Keysort punch card (Fig. 1) is used, the data from each quadrat being recorded on a separate card. Cards made of various grades of paper are available from the Royal McBee Inc., Port Chester, N. Y. The special design described below is available under the code name M.S.U. BOT. The margins of the card are divided into twenty-two large and six small fields which are used to record data for environmental and other pertinent variables. Each of the larger fields contains four holes which may be variously punched so that a total of fourteen combinations is possible. Hence, each factor to be considered may be divided into as many as fourteen classes, and each class assigned a code number. When more than fourteen classes are necessary, two or more fields may be combined. The smaller fields on the corners may be used to record factors which may be divided into a smaller number of possible classes.

A composite of two cards with the marginal fields labeled for a recent study is shown in Fig. 1. Specific field labels are not permanently printed on the card thus preserving more flexibility. Sorting of the cards for these edge-punched data is accomplished in the usual manner. The innovation which we have introduced can be seen in the center of the card in Fig. 1. Note that the card is marked off into 350 numbered squares which can be located by numbered ranks and rows along the margins. The number of each square represents the code number of a given species. Thus, if a species is present in the quadrat a hole is punched in the center of that species' code number square. A special punch

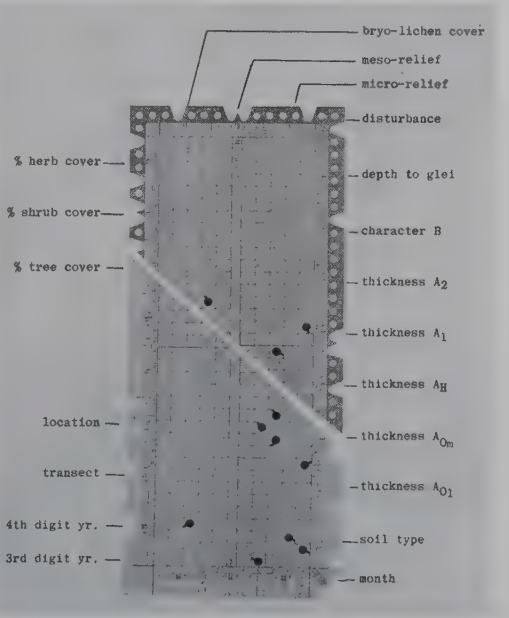

Fig. 1. A photograph of the M.S.U. BOT. design printed on the Royal McBee Keysort punch card. Twenty of the marginal fields have been allocated as indicated. The squares in the center represent the code numbers of up to 350 species on one card. In this hypothetical quadrat, eleven species are recorded as present. The photo is a composite of two cards, the upper one having colored margins. In studies involving more than 350 species, those with code numbers from 351 to 700, etc., are recorded on cards with colored margins.

[1] Supported by a grant from the All University Research Committee, Michigan State University. Publication no. 58-29 of Department of Botany and Plant Pathology.

(Royal McBee No. 5211) will punch both the code squares and the margins. Cards with different colored margins (see top portion of Fig. 1) can be purchased where more than 350 species are encountered. A plain buff card contains code numbers 1 to 350, a card with margins of another color numbers 351 to 700, etc. For studies involving more than 350 species in the sampled area, some quadrats would be represented by more than one card.

Per cent cover or abundance class of the species in each quadrat can be recorded since each code square is divided into eight sections (Fig. 2). A mark is placed in the appropriate section to indicate the cover or abundance class. Where greater accuracy is desirable, the hole can consistently be punched in a particular corner of the code square and the actual values written in the remaining block.

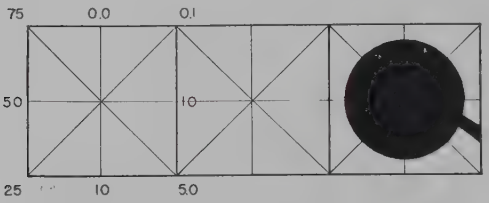

FIG. 2. An enlargement showing detail of the species code number squares from the punch card. On the left are the cover values represented by the eight lines radiating from the center of the square. On the right is a punched square with a line indicating a cover value between one and five per cent. These lines are usually made with a red pencil for easier reading. For greater accuracy the holes can be punched in a particular corner and the actual value written in the remainder of the square.

In order to sort for degree of co-occurrence of any two or more species, a template is made from a blank card by completely cutting out the particular species' code number squares. This template is then anchored against a T-square on a light table or a brightly colored surface, and each card passed over it for sorting. E.g., where degree of positive or negative association between two species is desired, the cards can be sorted into one of four piles: species A and B both present, A present, B present, neither present (see Cole 1949, 1957).

For small numbers of cards, instead of using the light table, the sorting needle can be used to separate the punched from the unpunched cards for any particular species. After carefully aligning the cards the needle is run slowly through the particular species' code number hole. Whenever the needle meets resistance the unpunched card can be lifted out of the pack by an upward motion of the needle tip and the card removed by hand. This separates the cards into "presence" or "absence" for the first species, and the resulting piles can then be sorted for a second species, and so on.

Since the cards contain quadrat data beyond simple species presence, they can be used to facilitate studies of a variety of ecological questions. E.g., association between species and particular environmental conditions, or regressions of species' cover or density on particular environmental variables, or multiple regressions of the cover of various combinations of species and environmental variables.

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AN EPIPHYTIC PRICKLY-PEAR CACTUS

A prickly-pear cactus (*Opuntia* sp.) is growing 7½ feet above the ground in the junction of the branches and the columnar trunk of a saguaro cactus (*Carnegiea gigantea*) in the desert southeast of Tucson, Arizona, approximately 2 miles north of Colossal Cave. Figure 1 shows the prickly-pear on the saguaro.

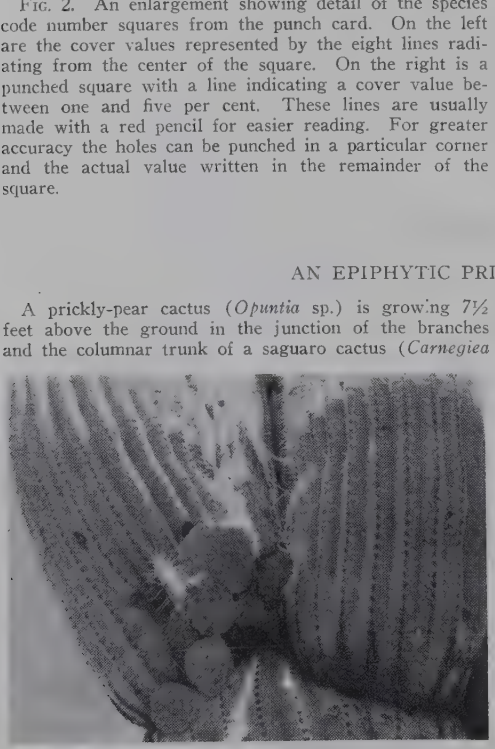

FIG. 1. A prickly-pear cactus growing in the branch junction of a saguaro cactus, southeast of Tucson, Arizona.

Organic debris and fine soil have collected in a crevice formed by a branch and the trunk of the saguaro. Observations following a rainstorm in the spring of 1958 indicate that moisture also collects there. Apparently the prickly-pear developed from a seed in bird droppings that fell into this crevice. It is believed that the prickly-pear's moisture and nutrition come from the soil in the crevice rather than from the tissues of the saguaro, even though the roots of the prickly-pear appear to be imbedded in the saguaro.

The prickly-pear made no measurable growth from September 13, 1956, to April 16, 1958.

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A Symposium on Population Ecology[1]

This volume comprises the papers and discussions from the Cold Spring Harbor Symposium held in June 1957. The conference was attended by some 150 scientists, about 40 of them from overseas. The Foreward tells us that "the purpose of this year's Symposium was to bring together in the informal setting of the Biological Laboratory ecologists, demographers, anthropologists, population geneticists, and mathematicians to discuss research problems, experimental procedures, and analytical techniques of common interest to the fields of ecology and demography." The papers on human populations, apart from the Introduction by L. C. Cole, are arranged in sections headed Historical Study (5 papers), Demographic Theory (4), Growth of Populations (3), Structure of Communities (3) and The Population as a Unit of Evolution (1). While they can be recommended as general reading, no further reference will be made to them here. Nineteen papers deal with animal populations.

The mixing of demographers with ecologists produced a few useful exchanges, but no great benefits can be seen from the printed account. On the other hand, the bringing together of propcnents of field ecology, laboratory experiments, and theory was evidently valuable and interesting. The relationships between these three types of study were a recurring topic of discussion. Cole introduces this subject and stresses that none of the three approaches should be disparaged. The observations on the role of mathematical models by Cole, G. E. Hutchinson, J. Neyman, J. Hajnal, J. G. Skellam, W. J. Cunningham and R. R. Sokal are complementary and provide a useful summary. D. Chitty deprecates the attachment of biological meaning to mathematical symbols. As a generalisation, this seems too sweeping, but it makes a useful point. Analogously, N. G. Hairston suggests that the response of a field population to experimental reduction may show the existence of density-dependent regulation, even although the factors concerned have not been identified.

There is some discussion of the concept of "environment." H. G. Andrewartha re-affirms his preference for thinking exclusively of the *individual's* environment. Th. Dobzhansky, A. J. Nicholson and Hutchinson oppose any such restriction and uphold the common and convenient use of the term with reference either to an individual or to a population. With reference to "Gause's hypothesis," T. B. Reynoldson and others discuss the concepts of "ecological niche" and "similar ecology." Nicholson argues that if "similar" allows for somewhat different needs or reactions, such as would normally be expected, two species of "similar ecology" must often be able to live together. Hutchinson devotes the greater part of his Concluding Remarks to a formal analysis of this hypothesis or principle and the conditions for its validity. He postulates that two species almost always have differences in their requirements which are detectable on close inspection. He cites a number of possible examples of the principle, and some types of exceptions, and suggests that the major groups of animals differ in their competitive relationships. He describes an ingenious deductive argument by R. MacArthur, leading to a method of extracting from community analyses, evidence whether or not the species occupy separate or overlapping niches. (The analysis of animal communities is not otherwise discussed except by P. Kontkanen, who compares three methods of association analysis, and by M. D. F. Udvardy with reference to birds.)

Cole introduces fluctuations with the reminder that some apparent population cycles are consistent with random variation. He attributes this to the complexity of factors affecting the populations having reached a level of secondary simplicity. Those who deal with the population cycles of rodents or insects in this Symposium favour deterministic explanations for the cases studied. S. Utida discusses population oscillations on a theoretical basis and by reference to his laboratory experiments with cowpea beetles (*Callosobruchus*) and their parasites. The experiments include one in which the host and two competing parasite populations continued in oscillation over 70 generations; his interpretation of this un-Gausian situation is that the fluctuation of the host favoured the two parasitic species alternately, one predominating at high host density, the other at low. Some aspects of population oscillations are considered by P. J. Wangersky and W. J. Cunningham, who discuss time lag in population models.

Rival explanations of natural control are well to the fore. The central issue is whether populations simply vary in abundance in accordance with changing environmental conditions, or are regulated about levels of density which vary with the environmental conditions by density-governing factors (Nicholson), also called density-dependent factors (Smith). The chief attempts to generalise refer primarily to insects. A paper by Andrewartha is largely based on a misconception of what is meant by density-dependent. He ranges many arguments in opposition to the view that populations are regulated by density-dependent factors, but does not demonstrate clearly what other explanation of natural control is conceivable. Sometimes he seems to suggest that natural control is too complicated to be explained, or alternatively that there is nothing to explain, only complex variations at random. His conclusion appears to be that an ecologist should observe the fluctuations, work out such statistics as the mean and the variability about it, and then extrapolate on a probability basis. It is of course legitimate to choose simply to describe fluctuations. But it is also legitimate to investigate how they are kept within the observed limits of density. L. C. Birch deals with the role of weather in determining distribution and abundance. "The discussion is built around a partly hypothetical model based on the influence of weather on the distribution and abundance of the grasshopper *Austroicetes cruciata* in Australia. The model is intended to illustrate how the fluctuations of weather in relation to spatial patchiness of the animal's environment, can regulate numbers in the sense of preventing unlimited increase and of avoiding the certainty, though not the possibility, of extinction." It is claimed that some populations simply vary in response to weather etc. and have no density-dependent regulation; they happen usually to escape extinction (at least in many of the habitats), and always to fall short of serious competition,

[1] Population Studies: Animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology, Volume 22, 1958. xiv + 437 pages, 147 fig. and 2 plates, tables. Cold Spring Harbor, New York: The Biological Laboratory. Price $8.00.

without the significant intervention of enemies or disease. Can anyone demonstrate numerically how diversity in terrain and weather can maintain such a result over long periods? Can the matter be clinched for this species by field experiments, as suggested by D. Pimentel in discussion? Birch fails to deal clearly with the fact that Nicholson and other supporters of density-dependence theories of regulation allow wide scope for the influence of weather upon the density-dependent factors and upon the results of their action. Incidentally, it would have clarified these arguments, including Cole's remarks, if "regulation" had been used only in this density-dependent sense.

A. Milne's article is a combative discussion of theories of natural control culminating in a Theory of his own. He holds that the ultimate control, when density reaches extreme heights, is intra-specific competition, but that density seldom reaches these heights because of the action of density-independent and other density-dependent factors. His development of these familiar ideas into a theory involves the propositions that the intensity of intra-specific competition maintains an exact relationship with population density and can therefore exert control unaided, while other density-dependent factors are imperfect and cannot "alone" exercise natural control. The argument supporting these propositions seems illogical.

Nicholson contributes an account of some of his laboratory experiments on blowfly populations, and a theoretically-based discussion of aspects of population regulation in general. His description of the fluctuations and compensatory responses of his *Lucilia* populations includes some interesting new material. The formidable strength of Nicholson's position lies in the amount of study he has devoted to the logical development of his system of ideas and their illustration in the laboratory. However, it still awaits the crucial process of detailed testing against a series of field populations.

In an interesting paper on his field studies, Reynoldson describes an investigation of the ciliate *Urceolaria mitra* which is epizoic on flatworms. He suggests density-dependent regulation by competition for suitable places on the "host," but probably only experiments, as suggested by Nicholson and Hairston, could really settle this. Reynoldson's account of the worm *Enchytraeus albidus* in sewage beds depicts a population mostly swept away from the system at intervals by apparently independent factors. F. Pitelka gives an account of the course of the 3-4 year cycle of *Lemmus trimucronatus* in N. Alaska; the lemmings rise to higher peaks in successive winters, until they destroy enough of their food and cover to expose themselves to predation, which is the main cause of their decline. P. L. Errington's discussion of the "10-year cycle," with reference chiefly to muskrats, exemplifies the difference between theoretical simplicity and actual complexity. The periodic decline of his muskrat populations seems to arise from mutual intolerance, but this occurs at quite different levels of density in different places and at different times. Errington is inclined to look for a background meteorological cycle, e.g. in ultra-violet radiation affecting the quality of the food. Chitty's progress report on his attempts to analyse the causes of the periodic declines in the numbers of *Microtus agrestis* in an area in Wales also presents a complicated picture. He postulates a non-infectious pathological condition associated with high density, effects of which continue for several years after the peak, and describes supporting evidence from laboratory experiments. He speculates that mutual strife may favour the spread of the factor causing the disease, while under most other circumstances normal animals are at an advantage.

Only two papers, by Dobzhansky and by R. C. Lewontin, deal primarily with the genetics and evolution of animal populations (Vol. XX, 1955, of Cold Spring Harbor Symposia was entirely devoted to Population Genetics); but, as Hutchinson remarks in concluding, frequent emphasis was laid on the changing nature of the populations dealt with.

The index contains subject entries but these are inadequate; author entries, on the other hand, are complete, including contributions to discussion and references.

While incidentally giving progress reports of some current research, this book will be useful primarily for the generous sample it provides of current ideas on population ecology.

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Animal Ecology Today[1]

The authors of most recent ecology books have had some sort of guiding philosophy which renders the contents of their books fairly consistent. Following some guiding philosophy also enables different authors to come to very different conclusions even when faced with the same data. Aware of this, Professor Bodenheimer has attempted to follow a different course. He readily admits that he has his own philosophy, but he has tried to present data independently of establishing pet hypotheses. At the same time, he attempts to give a picture of animal ecology today. To some extent he has been quite successful.

By presenting data in tabular form he has succeeded in putting a surprising number of facts into the book. Thus a particularly thorough survey of life tables and age distributions of different populations is given, omitting however a discussion of the intrinsic rate of natural increase, r. This is followed by a fine section on the relation between local climate and the incidence of various species.

The discussion of population regulation in general is excellent, if the reader is willing to do his own summarizing and ignore the semantic problems which have plagued ecologists for years. Basically, Bodenheimer admits that populations are more likely to decrease when very dense than when very sparse. However, he is unwilling to interpolate and conclude that intermediate population densities have an intermediate degree of reduction. Thus he believes that a growing population is not subject to continually increasing pressures; instead it grows unimpeded until, fairly suddenly, a large scale reduction sets in when the population has reached a sufficiently large size. This conclusion, though not new, may often be appropriate and goes far toward reconciling divergent views of density dependence.

Less satisfying is his dismissal of interspecific competition, as mathematically inconsistent and generally not important in nature. The only inconsistency in the competition equations lies in the biologist interpreting a constant K in the same fashion as he might for the logistic

[1] Bodenheimer, F. S. 1958. Animal ecology to-day. den Haag: Dr. W. Junk (Monographae Biologicae Vol. VI). 267 pp. 41 figs., 31 tables.

equation (and even this shows an incomplete understanding of the logistic). This merely shows that, as often happens, the pioneers of a subject use rather loose analogies; competition as a theory emerges unscathed. It is true that vigorous interspecific competition is rare in nature, but this is precisely what one would expect and by no means implies that it is unimportant in shaping communities. As a matter of fact, some very clear-cut cases of competition in pairs of species of barnacles, stem saw flies, Antillean flycatchers, and Australian pigeons leave no doubt that when competition would be expected, it often occurs.

The treatment of animal communities begins with a description of many collections and a conclusion, familiar to modern plant ecologists, that it is difficult to draw community boundaries. From this, he infers (P. 197) "The animal community is therefore a useful empirical and statistical conception, facilitating the description of animal life in various habitats but not a dynamic, superorganismic reality." What is unfortunate in this conclusion is that he apparently equates dynamic with superorganismic. This leads to two strange features in the book. First, although he no doubt rightly rules out a superorganismic concept as unscientific because untestable, he introduces, as central to ecology, an equally untestable and unscientific concept, the physiological life table. This deals with senility, the loss of ability to withstand environmental changes, in a completely constant environment! The second strange feature caused by equating the unscientific concept of a superorganismic community with the concept of a dynamic community is that Bodenheimer completely ignores such "dynamic" measurements as productivity and efficiency. Accepting the importance of these does not imply that the community has emergent properties which are not even in theory derivable from the properties of its components; it only implies that there are measurables such as productivity and efficiency which by their very nature involve whole communities. These are very profitable to study and help our understanding of other aspects of ecology; to omit them is surely not doing justice to the book's title.

In the section on interactions of environment and heredity, some other rather doubtful deductions are drawn. Bodenheimer seems to feel that most so-called adaptations are purely physiological in nature and not a result of protective coloration or other similar agents in natural selection. He runs into a double difficulty here. First he seems unaware of the excellent studies (for instance on melanic moths or desert *Peromyscus*, even in low light intensities) on the effectiveness of protective coloration, and hence concludes this has no protective value. Second, he is convinced that moving animals from one environment to another will affect precisely the change that advocates of natural selection would predict. This is not well established, but even if it were true it would only imply that adaptations are not the result of natural selection if one were also willing to admit that psysiological changes are mysteriously unaffected by natural selection. For it is not at all unreasonable that natural selection would produce appropriate physiological responses to environmental changes.

The book ends with a thoughtful and timely chapter on human population problems in the world today. As a whole, it leaves the reader with the impression that it is a valuable contribution which, however, must not be read uncritically and only partially represents animal ecology today.

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Field Biology and Ecology

Most fields of science are devoted to relatively circumscribed areas of subject matter and lend themselves quite readily to textbook treatment. Ecology is not in this category. The subject matter of ecology cuts across traditional boundaries in its concern with populations and communities and is extremely diverse. Moreover, many of the basic tenets of ecology are still not universally agreed upon by any means. Hence, it is understandably difficult to present the principles of ecology in brief and simple form. Principles of Field Biology and Ecology[1] is an attempt to combine the essentials of taxonomy, ecology, and animal behavior in a form that will be instructive to field biologists. Its approach is that of "enlightened natural history," as a stepping stone to the technical literature and methods of field biology and its related subjects. Presumably this book will have greater interest for students of wildlife management, conservation, and similar fields than those who will become professional ecologists.

The first chapter explains the nature of field biology and its application to biological problems. This is followed by a brief history of field biology in America from the time of the Colonial naturalists. Most of the emphasis is on the period before 1900, yet in the twenty pages devoted to this interesting topic there is only time to mention some of the major figures and one or two of their accomplishments. It is unfortunate that more space could not be allotted to this chapter. Very little mention is made of the influence of European biologists on field biology in America and the important developments in ecology, wildlife management and conservation since 1920.

The next seven chapters are devoted to taxonomic principles, ecological principles, terrestrial plant succession, aquatic plant succession, economic field biology, principles of population study, and principles of behavior study respectively. The treatment is mostly concentrated on field methods and systems of classification, rather than principles. For example, methods of determining population density, spatial distributions and age structure of populations are discussed in the chapter on principles of population study, but very little is said about the laws of population growth, competition or natural control of populations.

The quality of the text seems to be governed by the amount of material covered and the degree of simplification introduced. The chapter on terrestrial plant succession is very well done, with sixteen pages of text and illustration devoted to the process of plant succession from bare rock to climax forest. The descriptions are clear and sufficiently detailed to cover the topic adequately. The dangers of over-simplification are evident in the chapter on aquatic plant succession however. Oligotrophic lakes are characterized as "little-producing," eutrophic lakes as "good-producing" and dystrophic lakes as "bad-

[1] Benton, Allen H. & William E. Werner, Jr. 1958. Principles of field biology and ecology. New York: McGraw-Hill Book Company. vii + 341 pp., 120 figs. $6.50.

producing." There is no mention of mesotrophy or degrees of oligotrophy and eutrophy, and the resulting discussion is misleading and sometimes in error.

The chapter on behavior study is a commendable inclusion, although modern ethology is treated rather badly. Paraphrasing Lehrmann, the authors cite six specific objections to current ethological theory. As might be expected, most of these criticisms are directed toward the theory of innate behavior. Thus, the authors state, "By regarding traits as preformed and unchangeable, ethologists discourage inquiry into the actual source and development of the various aspects of behavior." While this view is common among psychologists, it is disappointing to find biologists who discredit the value of comparative studies and are content to brush aside the genetic and evolutionary implications of innate behavior.

The concluding two chapters discuss the use of biological literature and the choice and conduct of field problems. There is an eight-page glossary and a well-constructed index. The appendix includes, among other things, lists of key publications about subjects in field biology, sources of biological literature, a list of bibliographies, and a section on tools and techniques. The book is well-written and profusely illustrated. There are, perhaps, more halftones than are absolutely necessary; but most of them are of excellent quality, and the cost of the book is fairly reasonable. The companion volume, WORKBOOK FOR FIELD BIOLOGY AND ECOLOGY,[2] follows the basic outline of the text and contains descriptions of field techniques, selected laboratory and field exercises, and sample data sheets for each exercise.

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[2] Benton, Allen H. & William E. Werner, Jr. 1958. Workbook for field biology and ecology. Minneapolis: Burgess Publishing Company. x + 268 pp. $2.75.

RESEARCH ADVENTURES IN THE HUMAN ECOLOGY OF AN ATOLL[1]

A motivating love of environments in their panorama is the ecologists' inheritance from the naturalist. All too rarely the thrills are omitted in the scientific reporting, but in a new book, a scientific adventure by a science team among the native peoples of Ifaluk Atoll is described with charm and day-by-day enthusiasm. The interscience group under the Pacific Science Board, including M. Bates, D. Abbott, T. Arnow, F. M. Bayer, E. G. Burrows, R. R. Harry, and J. I. Tracey, searched for an atoll of maximum isolation in order to gain some knowledge and feeling for the relationship of man and nature. What they report is the rewarding experiences in a scientific expedition, in life in sophisticated communal culture, in self-understanding, and in the deep, peaceful, thunder of Pacific reefs.

The spirit of the atoll has been captured before, but rarely have the daily satisfactions in environmental science been allowed to show in a report of a serious study group. In this book there is something of Margaret Mead's cultural perspective, Nordoff and Hall's epic finality, Heyerdahl's narrative, the ecological breadth of Mayor, and the candid chronological accounts of Beebe. It is a good book for young science aspirants; for it is an account of the regular, simple pleasures in science without the formidable, popular clichés of discovery, invention, and applied service. The scientific results of the expedition are published elsewhere, but many facts and interpretations are presented in a general manner for the interest of reef scientist as well as for the layman. There is a bit of geology, hydrology, life history, human history, and anthropology. The book is organized in chronological sequence with each author writing half of the book. There are 28 pages of photographs.

Only a little space is given to describing the quantitative relationship of the human population to the atoll, but the conclusions are fascinating. In the last chapter, Abbott indicates that the annual yield of fish from the atoll to the 260 Micronesians is about 15 tons. From detailed food studies, it is suggested that protein supply from the reefs constitutes a limiting factor in determining the carrying capacity of the ecosystem. Neither the results of the other studies nor the conceptual objectives are made clear in the book, which in most aspects is a naturalist's account.

The candid account of the trip provides an example of the good and bad features of the type of expedition which has diffuse objectives and no strong organization. This book will be best appreciated by those already infected with tropical nostalgia from which, one suspects, there is no cure.

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[1] Bates, Marston & Donald P. Abbott. 1958. Coral island, portrait of an atoll. New York: Charles Scribner's Sons. 254 pp., plates. $4.95.

THE WERNER LÜDI FESTSCHRIFT[1]

The publication of this volume marks the 70th birthday of Dr. Werner Lüdi, since 1931 director of the famous Rübel Geobotanical Research Institute in Zürich and permanent secretary of the International Phytogeographical Excursions which have done so much to unify European plant geographers and ecologists. The new impetus that Cowles gave to plant ecology was taken up directly by Lüdi, and with the stimulus of Graebner's work on the north German heaths Lüdi made soil development a necessary part of plant succession studies. His later essay on "Methods of investigating succession in phytosociology" for Abderhalden's HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN (11(5):527-728, 1932) can still be read with profit by American ecologists for concepts, methods, and results achieved. At least once a year the doubt that climax vegetation is most productive creeps into the American plant ecological literature, but Lüdi systematized these doubts long ago for particular ecosystems. He did it on the basis of soils studies, which both Cowles and Clements neglected.

As an outgrowth of successful efforts to establish on the Schynigeplatte above Interlaken, in one of the most

[1] Welten, M. & H. Zoller (editors). 1958. Festschrift Werner Lüdi. (Symposium.) Veröffentlichen Geobotanischen Institutes Rübel in Zürich. Heft 33. 292 pp. Bern: Verlag Hans Huber. 26.80 SFr., $6.30.

scenically spectacular parts of Switzerland, a garden which should introduce the visitor to the wealth and beauties of Swiss alpine vegetation, Lüdi began experiments on fertilization of native vegetation. The aim was increase in productivity of Swiss hay meadows. Range fertilizers in the U. S. still have to test for possible adoption the methods of vegetation analysis used by Lüdi. Dr. Lüdi's interest in preservation of nature has been a natural outgrowth of his wonderful knowledge of Swiss mountain vegetation. In 1957 he led his 11th Course in Alpine Botany, with participants from 5 nations, over an itinerary which makes a mountaineering botanist who was not along extremely envious. Now Dr. Lüdi's continued devotion to the preservation of alpine vegetation finds additional scope in an official position with the Swiss federal government.

Many people who study succession eventually seem to feel the need for documented rather than inferential data, and like Lüdi they turn to pollen analysis—which unfortunately works on such an extended time scale that plant succession is not recorded, although vegetation change in response to changing climate is. Of the 23 papers in this volume just over half are on paleobotany, mostly palynology.

Three papers are taxonomic, leaving 10 on geobotany. The contributors number 9 Swiss, 4 Austrians, 3 Germans and one each from Ireland, Norway, Denmark, Poland, Finland, and France. One paper is in French, 3 in English, 19 in German.

Only a few of the papers can be discussed. Those not mentioned below are by Szafer, Firbas, Gams, Höhn-Ochsner, P. Müller, and Rytz on paleobotany and by Erdtman and Faegri on systematic botany (pollen morphology and hybrids in *Eriophorum*).

Braun-Blanquet and his collaborators give a well-documented picture of Mediterranean lagoon succession from 1915 to the present. Tüxen describes the vegetation of oligotrophic heath ponds over 30 years time in a nature reserve in northwestern Germany. New data on the ecology of various Sphagnum species aid in interpretation of the tabulated vegetation stands. The communities are finally assembled into a successional scheme which may or may not fit the current zonation. Frey discusses the effects of different systems of forest management on lichen flora and vegetation. Markgraf gives a picture of forest zonation in Turkey. Regel discusses the floristics of Lithuanian haylands.

The problem of plant species (including mosses) common to the arctic and alpine regions is elucidated by Kotilainen. Other chorological problems are suggested by Widder's new finds in Austria of *Carex punctata* Gaudin which has such a very disrupted area and by Zoller's discussion of *Stratiotes aloides* L. pollen from hypsithermal time in a now filled-in, eutrophic lake in the presently oligotrophic Tessin. The site is 150-200 km. distant from and over 1400 m. higher in elevation than the nearest present localities of the plant. Taxonomy of *Androsace* is discussed by Favarger, using cytological data, and thus bringing to bear on the systematics of alpine plants quite new techniques as compared to the time when Lüdi did the Primulaceae for Hegi's flora.

H. Wagner recognizes the difficulty of forcing plant community-types which have each a particular floristic composition, ecology, geographical distribution, and successional status into a linear system of phytosociological classification. He points out that ecological series run into geographical trouble; they are limited in scope by local geography. Classifications seem to be linear simply so they can be usable, and phytosociological classifications are floristic because thus they include ecology, chorology, and succession. Wagner makes some suggestions for classification of the central European forest plant communities and correlates the series of floristically defined alliances on different kinds of parent materials to coincide with the main types of soil formation found in central European forests. E. Schmid's essay suggests a complementary, synthetic method for geobotany. His views are limited by no divisions hitherto drawn within botany, but few people can fulfill his demands for such wide correlations of knowledge. It would seem from Doyle's updating of the 1949 IPE through Ireland that Braun-Blanquet and Tüxen's effort at a conspectus of Irish plant communities has stimulated further phytosociological work in Ireland.

The palynological papers are ecologically exciting. Pierre and Margita Villaret-von Rochow produce a model study of total vegetation development during post-Allerød time through a combination of exact knowledge of floristics, ecology, and vegetation of the immediate region, use of the great mass of central European data on forest history, and careful technique. Iversen gives a most interesting palynological substantiation of the relict nature of a Danish forest fragment. The pollen from raw humus soil horizons in the relict stand shows no plant succession but a maintenance of floristic character over the thousands of years since the early beech period. Welten further enlarges on the known ecology of the Schynigeplatte ecosystems with a study of pollen in alpine soil profiles.

Welten's paper adds to those which are changing classic concepts of soil formation and development. Williams in Russia has suggested that the Great Soil Groups which are so beautifully zoned parallel to climatic zonation from northern podsols to southern sierozems in Russia are *stages* of soil development since glacial times. Kubiena maintains that very many California soils are relicts of past climatic processes. Tedrow and his students are finding C^{14} ages of many thousands of years for the organic matter of arctic Alaskan soils. Dimbleby in England is using soil profile pollen to open up a whole new field of historical, archeological, and vegetation research. Now Welten has made an important contribution to soil history and has concluded that additions to the soil have built up the alpine soil profiles he studied—his soils have been built up, not weathered down. The soils have histories running back 5,000 years. Since Welten has not only C^{14} dates but pollen spectra as well, his few dates go a long way. Correlation of C^{14} dates with particular pollen events or species (such as *Ephedra*) enables him to set up a chronology for *all* his profiles. Since the ecology of the individual species and the vegetation they together form is well-known for this area, Welten can also say a good deal about past habitat conditions.

The conclusion seems obvious that absolute C^{14} dates are a supplement to good and well-interpreted pollen analyses. In fact Firbas' great pollen analytic work on central European forest history was written without C^{14} dates, although these substantiated his conclusions when they did appear. The primary work in such historical studies would seem to be ecological interpretation of pollen data.

An interesting conclusion of Welten's is that hypsithermal upward movement of timberline was insignificant in amount in his area. The attention of the Swiss, with their Alnetum viridis—Rhodoreto-Vaccinietum relation-

ships at timberline, should be drawn to southern Alaska where ecologically (and in part taxonomically) equivalent *Alnus crispa*-ericad community relationships may give clues for the interpretation of the Swiss, human-influenced ecosystems.

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Vegetation and Soil Development in the Swiss National Park[1]

The first publication on the vegetation and soils of the Swiss National Park was the now classic study by Braun-Blanquet and Jenny (1926) on "Vegetation development and soil formation in the alpine belt of the central Alps." The two monographs have now "created the basis for thorough experimental synecological investigations in the subalpine forest region [and in the alpine region]." In other words, Braun-Blanquet and his colleagues have believed that descriptive ecology must precede experimental. Most of the 28 monographs sponsored as scientific studies in the Swiss National Park have been largely inventories of various organism groups from nematodes and collembolans to lichens and mosses; and they have thus made a solid foundation for community studies. The flora of the canton of Graubunden where the National Park is located has been described in splendid detail by Braun-Blanquet and Rübel, the geology of the region is known, climatic stations have been recording data for many years, and accurate topographic maps are available, so ecological work can be done without the conventional handicaps.

In the U. S. we pride ourselves on our splendid National Park system, and we customarily say that one of its principal values is to provide natural areas for scientific study. In all the U. S. we have nothing to compare with the studies of their national park that the Swiss have made. It is probably easier to obtain time and money to study the ecology of the arctic slope of Alaska than it is to do a study in a national park in continental U. S. Yet surely our parks would be more persistently protected if they were more appreciated—if scientists and the general public could know more about them.

The present study contains 3 parts: Vegetation in 126 pages, microclimates in 8, and soils in 44. Much of the material has been published in excerpts before, but here it is all brought together.

The area studied has timberline at 2300-2400 m. elevation, the highest in Switzerland, and in truth this region is an enclave of peculiarly continental climate in the western Alps. *Pinus mugo, P. silvestris* ssp. *engadinensis, P. cembra,* and *Larix decidua* give a particular tone to these forests, which are quite different from the areas of more maritime climate where *Picea abies* dominates the landscapes.

The vegetation belongs to the order Vaccinio-Piceetalia, with alliances Pineto-Ericion which are seral communities over dolomite, Vaccinio-Piceion including the Abieto-Piceion sub-alliance on weakly podsolized brown forest soils of the montane zone in more oceanic climates, and the Rhodoreto-Vaccinion sub-alliance of the higher subalpine zone on acid soils and including the regional climax vegetation. Other, less common alliances in the same order include the Juniperion nanae on sites which do not support trees because of extreme but warm local climates, alluvial parent materials, or local topography such as avalanche tracks, and the Loiseleurieto-Vaccinion of still other wind-exposed, treeless sites.

The soils belong to two sequences, humus carbonate and podsol, with variations from the raw initial soils on calareous and siliceous detritus, respectively, to morcovered or brown forest-like humus carbonate soils or humus and iron podsols, gleyed or tending toward brown forest soil in grazed meadows. Analytical soils data are presented in numerous tables. These data almost uniformly lack bulk density and % skeleton figures. Without these the most exact soils analyses are not truly quantitative since one cannot calculate soil properties of the profile. However, the soils information given is excellent. A set of standard symbols is suggested as an aid in making more descriptive sketches of soil profiles.

An interesting point is the occurrence of one kind of plant community over such various soils as well-developed humus carbonate and iron podsols. Pallmann's concept of *analogous soils,* i.e. soils which offer similar conditions for plant growth, is shown to be ecologically necessary. Fortunately the authors have noted in their soils descriptions the space occupied by plant roots, so the concept of analogous soils can have meaning. In many of these soils plants seem to use only the A_0 and A_1 horizons.

The section on "microclimates" presents temperature data obtained by Pallmann's sucrose inversion method, the subject of a recent thesis by Murdock at Pullman. Unfortunately the term "microclimate" is used both for the climate inside a stand of vegetation and also for climatic variations due to relief. If the latter are termed local climates, the dependent and independent factors of microclimate and local climate can be separated and studied.

This monograph, like Braun-Blanquet and Jenny's earlier one, contains some of the best data we have on plant succession. In this study dated stream terraces provide an absolute chronology, but for all ecosystems the perhumid climate means that residual soils become progressively more acid with time as bases are leached out. In the Park the amount of water leaching through the soil profiles is from 200 to over 500 mm./year, increasing with altitude. Thus, the arrangement of different ecosystems in successional sequences is relatively straightforward; the more acid soils are older. This is a normal state of affairs for soils formed from rock weathered in place. Even so-called acidic rocks such as granites give a highly alkaline reaction when they first begin to weather and alkali ions are set free. Unfortunately not *all* leached soils become less acid with depth, but some reverse this trend. An explanation of this anomaly must be forthcoming to give a rational picture of soil development in the tropical and subtropical areas having such anomalous soils before soil formation will give automatically a timescale for plant succession studies. For example, some acid subsoil profiles have been considered relicts of a former climate, and present vegetation is assumed to be

[1] Braun-Blanquet, Josias, Hans Pallmann, & Roman Bach. 1954. Pflanzensoziologische und Bodenkundliche Untersuchungen im Schweizerischen Nationalpark und seinen Nachbargebieten. II. Vegetation und Böden der Wald- und Zwergstrauchgesellschaften (Vaccinio-Piceetalia). Ergebnisse der wissenschaftlichen Untersuchungen des schweizerischen Nationalparks, Band IV(N.F.), No. 28. 200 pp., 42 figs., 21 association tables. 20 SFr., $4.70.

returning such large amounts of bases to the surface as to reverse the effects of acid-leaching water.

A few random points may stimulate some interest. The summary of forest and soil successions is divided into seres differentiated by type of parent material (dolomite versus silicate, gravel versus sand alluvium), by slopes (north versus others), and by topography (long-lasting snow cover). Moraine or alluvium succession in this continental climate reaches the climax association Rhodoreto-Vaccinietum in less than 2000 years. Many sites never can develop climax vegetation but support persisting communities, which are seral on normal sites.

The 25 stands of the seral Ericeto-Pinetum silvestris are arranged in order of increasing altitude, and two continua of variation in floristic composition are pointed out. With increasing altitude there are more Vaccinio-Piceetalia species, and concurrently there are more Quercion pubescenti-petreae species with decreasing altitude. Similarly there is a continuous sequence of subassociations within the Mugeto-Ericetum when the 30 stands recorded in the association table are arranged in order of decreasing ratio of basiphile to acidiphile species. Because the drier subassociation and the colder one at the other end of the scale are both less favorable to the regeneration of *Pinus cembra*, the recognition of the 3 subassociations has applied value.

The monograph contains other ideas on vegetation classification. Floristic composition, not physiognomy is relied upon. For example, the alliance Loiseleurieto-Vaccinion, which is the alpine analogue of the Scandinavian lichen tundra, might be thought to belong to either the alpine tundra order Caricetalia curvulae or the subalpine forest order Vaccinion-Piceetalia. A decision is reached on the basis of 59 stand surveys which have 17 characteristic species of the latter but only 13 of the former order; the summations of the presence values for these characteristic species are 271 vs. 159; covers are in still wider ratio of 10:1.

The dynamic nature of vegetation and soil is not mentioned in the title of this monograph. However, the conclusions are grouped around the parallelism of vegetation development and soil formation, and a basic inventory of plant communities and soils forms the basis of the dynamic point of view which permeates the whole work.

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Agricultural Ecology[1]

G. Azzi, Professor of Agricultural Ecology in the University of Perugia, Italy, has worked in this field for some 45 years. He presents many valuable concepts and facts in this book. The aim of the author is to utilize the data of the physical environment in the solution of agronomic and economic problems in agriculture. The treatment is in four parts: agricultural climatology, the soil-unit and the climate-soil complex, the yield and ecological characteristics of cultivated plants, and factorial combinations and differential analysis of yield. A number of unusual approaches are used.

The author begins with the description and examples of his concept of "meteorological equivalents." This is defined as the degrees of temperature and quantity of rainfall which distinguish normal from abnormal conditions, either excessive or deficient. For example, to determine the equivalent of drouth for wheat in the month before earing he plotted 120 crop yields against amount of rainfall. Only poor yields were secured with rainfall below 25 mm., only good yields above 60 mm., and either poor or good yields between 25 and 60 mm. The mixture of poor and good yields in the intermediate portion is caused by interference or compensation of other factors. A line is drawn through the intermediate portion so that an equal number of poor and good yields will be above and below the line, which in this example is at 40 mm., the drouth equivalent. This equivalent can be used, not as a measure of the amount of yield, but as a criterion in the evaluation of the frequency of favorable and unfavorable conditions of rainfall or temperature. The monthly rainfall equivalents are worked out for a number of plants such as sugarbeet, potato, alfalfa, cotton, maize, wheat, grape, and the olive.

The climatic equivalents are used for making "climoscopes" and "climatic formulae." The former is a table listing rainfall and temperatures for the vegetative periods of plants. For wheat these periods are I autumnal, sowing and early growth; II winter, dormancy; III spring, growth to earing; and IV early summer, earing to maturity. The climatic formula summarizes for a series of years excess precipitation, deficient precipitation, excess temperature, and deficient temperature; so that EP^2_I means that twice in a series of years the precipitation was excessive in the first period, DT^2_{IV} temperature was deficient twice in the fourth period.

In the second part of the book climatic and soil characteristics are integrated into units, using maize as an example, for which there are 55 climate-soil units in Italy.

The "velocity-mass-structure" concept is the main theme of the third part of the book. This represents the relationship between development and yield of cultivated plants on one hand and the conditions of the natural and artificial environment on the other. By "velocity" is meant primarily the duration of the vegetative period, by "mass" the expansion or size of the plant; by "structure" the cellular nature such as size of cells, thickness of cell walls, etc. Italian wheats are classified into 5 velocity classes ranging from 40 to 55 days for development from earing to maturity; 5 mass classes ranging from 16 to 28 g; and 5 structure classes. The higher the class a variety is in the greater will be the yield under favorable conditions; the lower a variety is rated the greater will be the tolerance to unfavorable conditions.

The brief fourth part of the book concludes with this statement, "Agricultural Ecology thus offers a concrete basis for the organization of agricultural experimentation and for the solution of problems concerned with a better adaptation of crops to the physical environment." Following the text proper are 4 pages on Methodology, a brief glossary, and an extensive bibliography.

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[1] Azzi, Girolamo. 1956. Agricultural ecology. London: Constable & Co., Ltd.; Fairlawn, New Jersey: Essential Books. xv + 424 pp., 47 figs., num. tables. $7.20.

A Revised Edition of a British Ecology Textbook[1]

Dr. William Leach's tiny textbook of Plant Ecology is an interesting, though brief, survey of the most elementary principles of the science. It is intended for use in British schools, but the prefatory statement that British vegetation has been de-emphasized in this edition suggests the hope that it may be more widely used. However, virtually every point in the text is illustrated by examples drawn from British vegetation; the de-emphasis of the provincial format consists almost entirely of the elimination of short phrases, such as "in this country," "in British soils," and "in Great Britain." In at least one instance, the deletion of such a phrase was done without consideration of its effect on the already perplexing grammar, and resulted in the following enigmatic sentence (page 25): "In the case of coarse sand the particles are, usually almost entirely composed of quartz, they are insoluble in water and are chemically inert." Other rambling and involved sentences are not uncommon.

According to the preface, the fourth edition "has been completely revised and certain sections have been rewritten and enlarged." The claim to complete revision is exaggerated, but several grammatically complicated sentences of earlier editions have been rewritten; and here and there two or three words have been inserted to modify sentences, to extend them, or to explain a point more clearly. The introductory chapter is the only one that has been entirely revised. Previously, it presented a highly critical and almost pessimistic outlook on ecology. Now it is a brief, unevaluative account of the development of plant ecology, the author's opinion of the direction of ecological study, and a statement of advice to students wishing to undertake ecological studies. The section on temperature as an ecological factor has been entirely rewritten and extended (pages 14-15). A new paragraph was inserted into the section on altitudinal zonation to extend the concept to the vegetation of the extra-Britannic world (page 19). And a few lines were added to the discussion of edaphic factors to include calcium relations (page 34). The bulk of the text, however, remains unchanged, provincial, and Anglo-Clementsian. The 12 literature citations have also remained static. They are identical to those in the 1943 edition, and the latest is Sir Arthur Tansley's 1939 monograph on "The British Islands and their vegetation." The author attributes this lack of change to a corresponding lack of change in the scope and concepts of plant ecology. Few will accept this stand, for the concepts and scope of plant ecology have undergone considerable revision, refinement, and extension. The American automobile still has four wheels, two bumpers, and a windshield; but few of us would concede that it is largely unchanged since 1933. Thus, Dr. Leach's book, which was adequate in 1933, seems to me to resemble a Model A with a new coat of paint: revised but not timely. However, it does give a condensed and easily-read account of the ecological conditions of British vegetation and therefore is a valuable reference for the beginning ecologist and a quick refresher for the established ecologist.

[1] Leach, William. 1956. Plant ecology. 4th edn. London: Methuen & Co. Ltd.; New York: John Wiley and Sons, Inc. vii + 106 pp., 6 figs. $2.00.

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Sand Dunes of the Pacific Coast[1]

This work is essentially physiographic rather than ecological, the emphasis throughout being upon the processes of formation. As a geological memoir the role of vegetation in dune development is relegated to the background, which may in part explain the rather surprising omission of England from the list of countries from which significant contributions have been made to dune study. Correspondingly we find that dune vegetation is very cursorily dealt with, and whilst its role as a stabilising influence is recognised, little consideration is given to its modifying influence on the sand-bearing capacity of the wind. The author rightly criticises the over-emphasis, by some writers, of the part played by plants in dune formation. But because dunes, in deserts and on the coasts studied by the author, can be formed through other causes of diminution in the velocity of a sand-bearing wind, the importance of a cause of sand deposition capable of growth and augmentation should not be minimised.

The clue to these two opposing and rather parochial approaches probably lies in the human tendency to regard what makes for uniformity as more important than factors that tend to cause diversity. The author claims that the three elements of sand, wind and water combine to produce uniformity of structure and that vegetation introduces a fourth element that brings diversity and irregularity. Assuming the validity of this conclusion it affords an interesting contrast to some European dune systems where the physical factors are often responsible for irregularity and where the vegetation would appear to be the most unifying influence.

The text of this work comprises three sections of which the first, some 16 pages, is mainly concerned with the physical factors of the environment. The second part, of some fifty pages, treats of dune forms and processes whilst the largest section and the most important describes the various dune areas of the Oregon-Washington coast. In all, the dunes of thirty localities are described, four of which are north of Tillamook Head where, on an advancing coastline, the systems are simple and almost continuous with ridges parallel to the shore. The remaining twenty-six localities comprise systems of complex structure on a receding shoreline that present a diversity of combinations of erosion, stabilisation and rejuvenation. The whole account is illustrated by some admirable plans and photographs. The coastal area described is regarded by the author as having undergone a period of major submergence, followed by a slight rise with relative stability. The dunes south of Tillamook Head had essentially attained their furthest advance before the submergence whilst the dunes north of Tillamook Head are considered to have been built outwards from the line of the sea's furthest advance. The end of the period of the submergence is estimated as mid-post-Pleistocene.

[1] Cooper, William S. 1958. Coastal sand dunes of Oregon and Washington. Washington, D. C.: Geological Society of America Memoir 72, xii + 169 pp., 12 figs., 22 plates, 8 tables.

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CORRECTION

In the paper by E. F. Cook and J. R. Beer, entitled "A study of louse populations on the meadow vole and deer mouse," in Vol. 39, page 654, the graphs constituting Figures 5 and 6 should be transposed. The legends, however, are correctly numbered as they stand.